

University of Montana

## ScholarWorks at University of Montana

---

Graduate Student Theses, Dissertations, &  
Professional Papers

Graduate School

---

2000

### The dispersal /establishment dilemma: Effects of environmental variation on reproductive tradeoffs for an animal -dispersed plant

Wendy Parson

*The University of Montana*

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

**Let us know how access to this document benefits you.**

---

#### Recommended Citation

Parson, Wendy, "The dispersal /establishment dilemma: Effects of environmental variation on reproductive tradeoffs for an animal -dispersed plant" (2000). *Graduate Student Theses, Dissertations, & Professional Papers*. 10593.

<https://scholarworks.umt.edu/etd/10593>

This Dissertation is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

## **INFORMATION TO USERS**

**This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.**

**The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.**

**In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.**

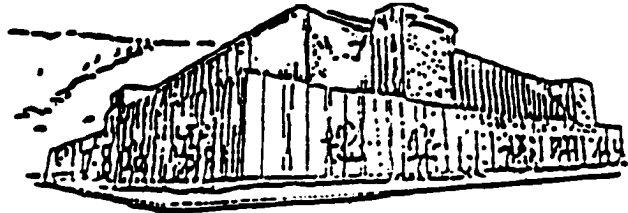
**Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.**

**Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.**

**Bell & Howell Information and Learning  
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA  
800-521-0600**

**UMI<sup>®</sup>**





Maureen and Mike  
MANSFIELD LIBRARY

The University of **MONTANA**

---

Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

*\*\* Please check "Yes" or "No" and provide signature \*\**

Yes, I grant permission ✓  
No, I do not grant permission       

Author's Signature Wendy Parson

Date 4-27-00

Any copying for commercial purposes or financial gain may be undertaken only with the author's explicit consent.



**The dispersal / establishment dilemma: effects of environmental  
variation on reproductive tradeoffs for an animal-dispersed plant.**

by

Wendy Parson

B. S. Wildlife Science, University of Washington


Presented in partial fulfillment of the requirements for the

Degree of Doctor of Philosophy

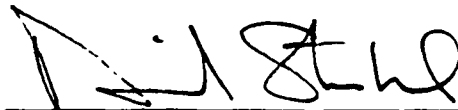
The University of Montana

2000

Approved by:



Chairman, Board of Examiners



Dean of the Graduate School

4-28-2000

Date

UMI Number: 9968495



---

UMI Microform 9968495

Copyright 2000 by Bell & Howell Information and Learning Company.

All rights reserved. This microform edition is protected against  
unauthorized copying under Title 17, United States Code.

---

Bell & Howell Information and Learning Company  
300 North Zeeb Road  
P.O. Box 1346  
Ann Arbor, MI 48106-1346

## ABSTRACT

Parson, Wendy: PhD: Spring 2000

Division of Biological Sciences

The dispersal / establishment dilemma: effects of environmental variation on reproductive tradeoffs for an animal-dispersed plant (151 pp.)

Advisor: Thomas E. Martin, PhD *TEM*

Plant reproductive strategies may evolve from fitness tradeoffs between seed dispersal and seedling establishment. Small crops of large seeds generally are not dispersed as far as large crops of small seeds, but large seeds contain more reserves for seedling establishment. However, selection pressures imposed on these traits may vary among environments. This study examined the extent and consequences of environmental variation in the reproductive strategy of a fleshy-fruited plant (*P. virginiana*) for offspring recruitment.

From 1996 to 1999, *P. virginiana* fruit crop and seed traits were measured for plants randomly sampled in moist riparian or dry slope habitat. The consequences of variation in *P. virginiana* location, seed size and seed number for seed dispersal were estimated by collecting seeds in seed traps. *P. virginiana* seed and seedling distributions were manipulated with respect to seed size, density, distance from adult canopies, habitat, protection from seedling predators and amount of soil moisture received by seedlings.

*P. virginiana* produced larger crops of smaller seeds in riparian versus slope habitat. Frugivores preferred large fruit crops (both habitats) and relatively small seeds (slope habitat). In riparian habitat, seed deposition by frugivores and seedling establishment were greater away from rather than under *P. virginiana* canopies. Large seeds were more likely to be predated than small seeds in both habitats, but predation of seeds and seedlings was most predominant in riparian habitat. The production of small, dispersible seeds may be critical in this habitat to move offspring away from the negative effects of parent plants. In contrast, seed deposition and seedling establishment on slopes were greatest under canopies. Large seeds were positively associated with seedling growth, and desiccation was the predominant seedling mortality factor. In this habitat, only seedlings from small seeds experienced increased survival when provided with supplemental water. Thus, the importance of large seeds for seedling establishment on slopes may override the negative effect on the likelihood of seed dispersal. Because slope plants have overall positive effects on offspring establishment, dispersal of offspring may be relatively unimportant or even undesirable.



## ACKNOWLEDGEMENTS

I thank the members of my graduate committee: Ray Callaway, Bette A. Loiselle, David Patterson and Anna Sala for their generous time and advice. In particular, I thank my graduate advisor and mentor, Thomas E. Martin, for teaching me to write clearly and concisely, to understand “why we should care” about research, and to think like a scientist. The lessons that I have learned from Tom’s “teas” and from Tom’s many other graduate students will stick with me not only as an ecologist, but as someone who is interested in learning and conveying information of any kind. I especially thank Alexander V. Badyaev for his helpful critical advice and moral support. I thank Daniel B. Miles for helping me plant thousands of seedlings each spring, often in a downpour. For financial support, I thank The University of Montana for a teaching assistantship and pre-doctoral fellowship, and the National Science Foundation for a graduate research fellowship. I thank my parents, William W. Parson and Polly C. Parson, for instilling in me a love of reading, nature and science, and for encouraging me to choose whatever career path I most desire. Finally, I thank my fiancé, William D. Bain, for his friendship and love for the past eight years, and his ability to make me laugh.

## PREFACE

When I first entered graduate school, I was intrigued by the messiness surrounding our understanding the evolution of animal-dispersed plants. Current research had demonstrated that the relationship between plants and their frugivores was often “diffuse” rather than tightly co-evolved. Evolutionary responses of plants to dispersers may be slowed by many factors, including phylogenetic constraints on reproductive traits and environmental pressures unrelated to seed dispersal. I realized, however, that an inadequate geographic perspective may cause the selection pressures imposed by frugivores to seem weaker than they really are. Selection that appears weak at the level of species, for example, may in fact be strong at the level of populations (Thompson 1994). Thus, I determined to address part of my dissertation research to the question: are dispersal pressures consistent enough within *local* environments to influence plant reproductive strategies?

Any question concerning local adaptations must examine the relative fitness of all phenotypes that are likely to occur in a given environment. Thus, I examined two alternative reproductive strategies that are likely to be adopted by maternal plants: the production of many, small seeds versus fewer, larger seeds. These two strategies can influence seed dispersal and seedling establishment in different ways. As a result, my dissertation research became an attempt to determine whether seed size and number variation is adaptive for seed dispersal versus seedling establishment.

Each of the following chapters has been written as an independent paper to be submitted for publication. Chapter One addresses the extent of environmental variation in seed size and number for a plant that grows in contrasting habitats. Chapter Two examines frugivore preferences and subsequent seed dispersal patterns in each of these habitats. Finally, Chapter

Three examines the consequences of both seed size and number and seed dispersal patterns for offspring establishment. As a whole, these chapters link patterns of local variation in plant reproductive traits with current pressures on offspring dispersal and establishment. Ultimately, I believe they reveal how an animal-dispersed plant resolves reproductive tradeoffs in a manner that is currently adaptive.

*References:*

Thompson, J. N. 1994. The coevolutionary process. Univ. of Chicago Press, Chicago.

## TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS .....	iii
PREFACE .....	iv
LIST OF TABLES.....	vii
LIST OF FIGURES .....	ix
CHAPTER 1: Environmental Variation in Seed Number and Size of a fleshy-fruited plant.....	1
METHODS .....	5
RESULTS .....	9
DISCUSSION.....	11
SUMMARY.....	16
LITERATURE CITED .....	19
CHAPTER 2: Seed Size, Number and Habitat of a Fleshy-Fruited Plant: Consequences for Seed Dispersal.....	41
METHODS .....	45
RESULTS .....	55
DISCUSSION.....	57
SUMMARY.....	62
LITERATURE CITED .....	63
CHAPTER 3: Seed Size, Number and Habitat of a Fleshy-Fruited Plant: Consequences for Seedling Establishment. ....	88
METHODS .....	92
RESULTS .....	104
DISCUSSION.....	108
SUMMARY.....	116
LITERATURE CITED .....	119

## LIST OF TABLES

### CHAPTER 1

<b>Table 1:</b> ANCOVA results for habitat, year and canopy volume effects on seed number, size and mass.....	30
<b>Table 2:</b> Paired t-test results for between-year differences in seed number, size and mass .....	31
<b>Table 3:</b> ANCOVA results for year, crop size and canopy volume effects on seed size .....	32

### CHAPTER 2

<b>Table 1:</b> Number of seed traps or quadrats placed in riparian habitat.....	70
<b>Table 2:</b> Number of seed traps or quadrats placed in slope habitat.....	71
<b>Table 3:</b> Likelihood of visitation by frugivores, seed dispersers or seed predators .....	72
<b>Table 4:</b> Logistic regression results for the likelihood of visitation by frugivores, seed dispersers or seed predators .....	73
<b>Table 5:</b> Number and proportion of seeds processed or predated per plant .....	74
<b>Table 6:</b> Kruskal-Wallis test results for habitat and year effects on the number of processed or predated seeds .....	75
<b>Table 7:</b> Spearman's Correlations between crop size, seed size or canopy size and the number of processed or predated seeds.....	76
<b>Table 8:</b> Number and proportion of seeds (a) processed from plants visited by frugivores or (b) predated from plants visited by predators.....	77
<b>Table 9:</b> Partial regression coefficients for habitat, year, crop size, seed size and canopy volume effects on seeds (a) processed from plants visited by frugivores or (b) predated from plants visited by predators.....	78

### CHAPTER 3

<b>Table 1:</b> Kruskal-Wallis test results for distance, density and orientation effects on seed removal rates .....	127
<b>Table 2:</b> Kruskal-Wallis test results for distance, density and orientation effects on seedling survival .....	128
<b>Table 3:</b> ANOVA results for habitat, distance and seed size effects on seedling growth .....	129
<b>Table 4:</b> ANOVA results for habitat, water treatment, distance and seed size effects on seedling growth.....	130

<b>Table 5:</b> ANOVA results for habitat, protection treatment and distance effects on seedling growth .....	131
--	-----

## LIST OF FIGURES

### CHAPTER 1

<b>FIGURE LEGENDS</b> .....	33
<b>Fig. 1:</b> Error bar chart of predawn xylem pressure potential versus habitat .....	34
<b>Fig. 2:</b> Error bar chart of estimated marginal means for (a) crop size and (b) seed size versus year and habitat .....	35
<b>Fig. 3:</b> Error bar chart of between-year differences in (a) crop size and (b) seed size .....	36
<b>Fig. 4:</b> Partial regression plots of crop size versus seed size in slope habitat in (a) 1996, (b) 1997 and (c) 1998 .....	37
<b>Fig. 5:</b> Scatter plot of seed width versus length .....	38
<b>Fig. 6:</b> Error bar chart of estimated marginal means for (a) seed mass and (b) fruit mass versus year and habitat .....	39
<b>Fig. 7:</b> Line graph of precipitation versus month .....	40

### CHAPTER 2

<b>FIGURE LEGENDS</b> .....	79
<b>Fig. 1:</b> Scatter plot of crop size versus predated seeds .....	81
<b>Fig. 2:</b> Partial regression plot of crop size versus processed seeds .....	82
<b>Fig. 3:</b> Error bar chart of the difference between average seed size and (a) processed or (b) consumed or depulped seed size versus habitat or year .....	83
<b>Fig. 4:</b> Error bar chart of the difference between average seed size and processed seed size versus year .....	84
<b>Fig. 5:</b> Line graphs of seed densities versus (a) distance from <i>P. virginiana</i> , (b) distance and orientation, and (c) distance from <i>P. trichocarpa</i> .....	85
<b>Fig. 6:</b> Bar chart of processed seeds versus distance from <i>P. virginiana</i> .....	86
<b>Fig. 7:</b> Radar chart of number of frugivores departing as a function of direction .....	87

### CHAPTER 3

<b>FIGURE LEGENDS</b> .....	132
<b>Fig. 1:</b> Error bar charts of seed detection versus (a) year, (b) distance and (c) orientation .....	137
<b>Fig. 2:</b> Error bar charts of seed removal rates versus (a) year and (b) distance .....	138

<b>Fig. 3:</b> Error bar chart of the difference between large and small seed removal .....	139
<b>Fig. 4:</b> Error bar charts of seedling emergence versus (a) distance and (b) orientation ....	140
<b>Fig. 5:</b> Error bar charts of seedling survival versus (a) year, (b) distance, 1998 and (c) distance, 1999 .....	141
<b>Fig. 6:</b> Error bar charts of seedling mortality in (a) 1998 and (b) 1999 .....	142
<b>Fig. 7:</b> Error bar chart of seedling emergence versus seed size and habitat.....	143
<b>Fig. 8:</b> Error bar charts of (a) height growth or (b) number of leaves versus seed size and habitat.....	144
<b>Fig. 9:</b> Error bar charts of total growth of (a) 10-week or (b) 13-month old seedlings versus seed size and habitat .....	145
<b>Fig. 10:</b> Error bar charts of seedling (a) emergence or (b) survival versus water treatment and habitat .....	146
<b>Fig. 11:</b> Error bar charts of seedling survival versus seed size and water treatment in (a) riparian and (b) slope habitat.....	147
<b>Fig. 12:</b> Error bar chart of predawn xylem pressure potential versus distance and habitat .....	148
<b>Fig. 13:</b> Bar chart of seedling establishment versus seed size and habitat.....	149
<b>Fig. 14:</b> (a) Bar chart of seedling establishment and seed deposition or (b) seedling recruitment versus distance and habitat.....	150
<b>Fig. 15:</b> Line chart of the relative importance of seed size and number for dispersal or establishment versus parental environment.....	151



# **CHAPTER 1**

**Environmental Variation in Seed Number and Size of a fleshy-fruited plant.**

## INTRODUCTION

The conflict between offspring quantity and quality (e.g., size, or the amount of resources invested in each offspring) is a fundamental life history tradeoff for many organisms, including plants, invertebrates and vertebrates (Smith and Fretwell 1974; Stearns 1976, 1992). However, the optimal solution for offspring size versus number may differ among environments (Willson 1983; Fenner 1985; Schlichting 1986; McGinley 1987). Optimal seed size, for example, can vary within plant species, populations or individuals as a result of environmental conditions or patterns of resource allocation (e.g., Capinera 1979; Cavers and Steel 1984; Gross 1984; Stanton 1984; Wulff 1986; Michaels et al. 1989; Ouborg and Van Treuren 1995). Variation in seed size can influence other genetically- or phenotypically-correlated reproductive traits, such as the number, structure and composition of fruits or seeds (e.g., Christie and Kalton 1960; Ogden 1974; Willson and Price 1980; Galen and Weger 1986; Marshall 1986; Venable and Brown 1988; McGinley 1989; Fox 1990; Kang and Primack 1991; Stephenson 1992; reviewed in Roff 1992; Baker et al. 1994). Thus, studies of environmentally-caused variation in offspring size and correlated traits such as offspring number are essential for understanding the evolution of reproductive strategies.

Variation in seed size versus number can reflect a compromise between maximized seed dispersal (i.e., movement of seeds away from parent plants) versus maximized seedling establishment (e.g., seed germination and seedling emergence, growth and survival). Large crops of small seeds, for example, may be an adaptation to increase dispersal because of the increased mobility of small seeds and the large numbers of offspring that can potentially disperse (Ridley 1930; Baker 1972; Howe 1980; Howe and Richter 1982; Morse and Schmitt 1985; Hoppes 1988; Sallabanks 1992). Such a strategy may be favored when seed and seedling mortality primarily result from distance or density-dependent factors (e.g., predation or competition; Janzen 1970; Connell 1971; Platt

1976; Antonovics and Levin 1980; Kaspari 1993; Barot et al. 1999). In contrast, relatively small crops of large seeds can increase seedling establishment and may be favored when offspring mortality primarily results from limitations in critical resources (e.g., moisture, nutrients or light; Baker 1972; Foster 1986; Howe 1990; Sultan 1996; Milberg et al. 1998). Of course, many environmental factors may simultaneously impose pressure on plants to increase both dispersal and establishment. High levels of density-dependent intraspecific competition can favor increased dispersal, for example, but also can favor increased seed size as a result of resource limitations. In general, resolution of the seed size/number conflict may depend on the relative strength of selection for dispersal versus establishment, which in turn will vary with environmental conditions (Capinera 1979; Howe et al. 1985; Ganeshaiah and Uma-Shaanker 1991; Hammond and Brown 1995; Schupp 1995). However, no studies have empirically examined how seed size and number vary for conspecific plants in environments that differ in the strength of selection for dispersal versus establishment.

I studied seed trait variation in common chokecherry (*Prunus virginiana*), a fleshy-fruited North American tree that grows in two contrasting habitats (i.e., riparian versus slope) in western Montana. Riparian habitat contains high densities of potential intraspecific competitors and seed predators (i.e., small mammals) under and near adult *P. virginiana* (Parson, pers. obs.). Thus, riparian habitat may impose high selection pressure on seed dispersal. In addition, the moist nature of riparian habitat may impose relatively weak selection for characteristics that favor seedling establishment. Slope habitat has fewer potential competitors or predators than riparian habitat but is relatively dry. Thus, slope habitat may impose high selection pressure on seedling establishment and relatively weak selection pressure on seed dispersability.

The following alternative hypotheses were tested in this study. **(1) Dispersal Limitation**

*Hypothesis:* plants should produce large numbers of small seeds in environments in which seed dispersal is the most limiting factor for offspring recruitment (e.g., *P. virginiana* in riparian habitat). Fruit size is commonly related to seed size, and thus also may be relatively small in this environment. However, the pulp-to-seed ratio (i.e., ratio of net fruit size to seed size) may be relatively large to attract dispersers (Howe and Vande Kerckhove 1980; Herrera 1981; Sallabanks 1993). In addition, selection by frugivores may favor seeds that increase in length faster than width because of potential gape width limitations on fruit consumption and seed dispersal (Wheelwright 1985, Jordano 1987; Debussche and Isenmann 1989; Mazer and Wheelwright 1993). **(2) Establishment Limitation Hypothesis:** plants should produce small numbers of large seeds in environments in which seedling establishment is the most limiting factor for offspring recruitment (e.g., *P. virginiana* in slope habitat). Because seed dispersal is not as important in this environment, plants should invest less energy in fruit pulp (i.e., pulp:seed ratios should be low), and may not exhibit size-dependent changes in the allometric relationship between fruit or seed width and length. **(3) Resource Limitation Hypothesis (short-term response):** seed size and number are directly influenced by resource levels available to parent plants, rather than by the relative importance of dispersal and establishment for offspring recruitment. Thus, plants should produce large numbers of large seeds and fruits in resource-rich environments (e.g., *P. virginiana* in riparian habitat) and small numbers of small seeds and fruits in resource-poor environments (e.g., *P. virginiana* in slope habitat). In addition, total reproductive biomass (i.e., fruit crop size\*fruit mass) is likely to be greater in resource-rich environments than in resource-poor environments. Because seed size and number are likely to be influenced by resource availability (i.e., levels of soil moisture) in the months immediately before and during seed development, dry years (i.e., years with lower-than-average levels of precipitation during this time) should be associated with reductions in fruit crop size or seed size, and wet years should be associated with

increases in fruit crop size or seed size. For all hypotheses, no *a priori* predictions were made regarding size-number correlations within environments, since a positive correlation may be apparent if plants differ in their ability to acquire resources, but a negative correlation may be apparent in particularly resource-limited conditions (e.g., slope habitat, where differences in resource acquisition may be unimportant relative to differences in reproductive allocation).

## STUDY AREA AND METHODS

All sampling of *P. virginiana* was conducted in the foothills of the Rocky Mountains of western Montana (~1000m elevation). *P. virginiana* is a shrubby tree that produces fleshy fruits with hardened endocarps (i.e., inner walls) that enclose single seeds until germination. The fruits are particularly attractive to avian frugivores, which consume the fruit pulp and excrete, regurgitate or drop the seeds. Primary frugivores on *P. virginiana* in western Montana are *Bombycilla cedrorum* and *Turdus migratorius* (Parson, pers. obs.). By removing fruit pulp, these frugivores are likely to have a positive effect on *P. virginiana* seed germination (Meyer and Witmer 1998); thus frugivore preferences may impose selection pressures on the size and number of seeds produced. In western Montana, *P. virginiana* typically occurs in two distinct habitat types: scattered in clumps on relatively xeric south to west-facing slopes (generally on exposed, rocky faces) and as part of a continuous band of mesic vegetation on the edges of riparian corridors. Thus, *P. virginiana* individuals may experience markedly different conditions for seed dispersal and offspring establishment, and reproductive tradeoffs can be compared among plants growing in the two unique environments.

To determine whether riparian and slope habitats differ in levels of abiotic stress, a pressure bomb was used to measure pre-dawn water potentials (MPa) of 15 fruit-bearing *P. virginiana* in each

habitat. All sampling was performed in August 1998 from 3:00 A.M. to 6:00 A.M. in dry conditions.

Seed-related traits were measured from 1996 – 1998 for plants (i.e., clonal clumps of individual stems spaced less than 0.5 meter apart) randomly sampled from 21 sites in or near the Bitterroot Valley of western Montana. In 1996, plants from only 15 of the 21 sites were sampled, and in 1998, two of the 21 sites were not sampled because plants sampled previously in these sites did not produce fruits. Sites consisted of clusters of *P. virginiana* that were growing at least 3.2 km away from other clusters that were sampled. Within sites, one to nine plants were randomly selected (mean = 3; number selected was roughly proportional to number of plants present), and the habitat in which they occurred was classified as riparian (i.e., 45 plants in or on the edge of riparian corridors) or slope (i.e., 44 plants on slopes away from the edge of riparian corridors; only two sites contained plants from both habitat types).

Total fruit crop size was estimated for individual plants in all three years by complete counts (when the total number of fruits was less than 200), counts of fruits in increments of 10 (for fruit crops of 200-1000 fruits), or counts of fruits in increments of 50 (for fruit crops greater than 1000 fruits). Incremental counts were calibrated with complete counts periodically to ensure that they remained accurate. All counts were performed three times and averaged to obtain total fruit crop size. Number of fruits per raceme (an estimate of fruit production on a relatively small scale) was estimated in 1996 and 1997 by averaging the total number of fruits produced by 10 randomly-selected racemes per plant. Canopy size (i.e., canopy height, width and depth) was estimated for each plant to the nearest 0.5 m.

At the beginning of the dispersal period in late August (i.e., when most fruits on plants are ripe), 15 fruits were sampled randomly from the middle of racemes located in the middle (from top to bottom) of each plant canopy. Digital calipers were used to measure dimensions (width, length and depth) of all collected seeds (i.e., endocarps) and dimensions of a subsample of collected fruits (1997 and 1998 only) to the nearest 0.01 mm (averages were calculated from 3 repetitions of each measurement). To determine the relationship between seed volume and seed weight, 150 purchased seeds (collected in 1997 in western Montana and Idaho) were measured and weighed to the nearest 0.001 g. In addition, dimensions and fresh and dry weights were obtained for 99 fruits and seeds collected from field sites in 1999 (5 fruits per plant, 9 plants per habitat). Linear regression results of seed volume vs. dry weight ( $wt = 0.00088 * vol$ ;  $R^2 = 0.90$ ;  $N = 249$ ) and fruit volume vs. fresh weight ( $wt = 0.00088 * vol$ ;  $R^2 = 0.91$ ;  $N = 89$ ) then were used to estimate weights of all collected seeds and fruits. In the analyses described below, seed trait variation was examined primarily with seed (i.e., endocarp) volume, which may function both as an indication of attractiveness to dispersers or predators and as an indication of seed or seedling vigor. Seed and fruit volume were calculated with the formula for an ellipsoid ( $volume = (1/6) * \pi * l * wd * ht$ ), which approximates the shape of a chokecherry seed. Measurements of purchased seeds with sizes typical of those found in riparian habitat ( $\bar{x} \pm 1 SD = 96.63 \pm 29.50 \text{ mm}^3$ ) indicated that endocarp size was strongly positively associated with the mass of the seed inside the endocarp (i.e., embryo + endosperm;  $R^2 = 0.80$ ;  $N = 49$ ;  $P < 0.0005$ ).

Measurements of precipitation were obtained from the Western Regional Climate Center Web Page ([www.wrcc.dri.edu/index.html](http://www.wrcc.dri.edu/index.html)) for Missoula WSO AP, MT (i.e., the weather station nearest to all study sites). Specifically, the NCDC 1961-1990 monthly normals were used as indications of average monthly precipitation, and monthly precipitation listings for 1996 – 1998 were used to obtain monthly summaries of precipitation.

*Data Analysis:* To obtain normally-distributed variables for statistical analysis, seed number (i.e., fruit crop size and number of fruits per raceme), canopy volume, fruit size (i.e., fruit volume – seed volume), and seed width, length and depth were  $\log_{10}$ -transformed, and seed volume was square-root-transformed. An  $\alpha$ -level of 0.05 was used for all tests.

Difference in pre-dawn xylem pressure potential between habitats was tested in a Simple Factorial ANOVA with habitat and day as fixed main effects (the two-way interaction was nonsignificant and was removed from the final model). Dependent fruit crop and seed trait variables (average values per plant) were tested in General Factorial ANCOVA's with habitat and year as fixed main effects and plant canopy volume as a covariate (all two-way interactions were nonsignificant and were removed from final models; seed or fruit width, length and depth were tested in multivariate ANCOVA's). Similar results were obtained from ANCOVA's conducted for the subset of plants sampled in all three years (Parson, unpubl. data). These additional tests ensured that results were not influenced by the inclusion or absence of particular plants in different years. Plant canopy area and volume were compared between habitats in Independent Samples T-tests; p-values were multiplied by 2 to provide a Bonferroni correction for multiple tests. For plants sampled in more than one year, fruit crop size, seed size and total seed mass were compared between years for each habitat in paired t-tests (all years were not tested simultaneously because the small number of plants sampled in 1996 limited the total sample size and may have substantially reduced statistical power; to provide Bonferroni corrections, p-values were multiplied by 6 for fruits/plant, seed volume/plant and total seed mass/plant, and multiplied by 2 for fruits/raceme). Correlations between seed size and seed number or fruit size were tested in General Factorial ANCOVA's with year as a fixed main effect, canopy volume as a covariate and seed number or fruit size as a covariate (p-values were multiplied by 2 to provide a Bonferroni correction because habitats were tested separately; correlations within years were



tested separately in linear regressions if year or the interaction between year and the covariate were significant in the original model). Ratios of pulp-to-seed fresh mass and dry mass were analyzed in nested General Factorial ANOVA's in which plant (a random effect) was nested within habitat (a fixed effect; data available for 1999 only). The allometric relationship between seed length and width was tested for each habitat by comparing slopes from partial regressions of seed length versus width in which year and canopy volume were held constant (p-values were multiplied by 2 to provide a Bonferroni correction). Wilcoxon signed-rank tests were used to compare monthly precipitation between years (p-values were multiplied by 3 to provide a Bonferroni correction), and to compare monthly precipitation to 30-year average precipitation levels (p-values were multiplied by 3 to provide a Bonferroni correction).

## RESULTS

*Abiotic stress:* During the 1998 growing season, available soil moisture (i.e., pre-dawn xylem pressure potentials in mature plants) was lower on slopes than in riparian areas ( $F_{1, 29} = 19.78$ ;  $P < 0.0005$ ; Fig. 1).

*Seed size versus number:* In all three years, *P. virginiana* plants in riparian corridors produced larger crops (with respect to both fruits/plant and fruits/raceme) of smaller seeds than similarly-sized plants on slopes (Fig. 2; Table 1). Thus, seed size and fruit crop size were inversely related between habitats. Seeds also differed between habitats in width, length and depth ( $F_{3, 175}$  (approximated with Pillai's Trace) = 22.33;  $P < 0.0005$ ). Plants in riparian and slope habitat did not differ from each other in canopy area ( $t = 0.52$ ;  $df = 85$ ;  $P = 1.00$ ) or volume ( $t = 1.27$ ;  $df = 85$ ;  $P = 0.42$ ), measures of plant size that may reflect the energy available to plants for fruit production.

In paired t-tests, fruits per plant, fruits per raceme and seed size did not vary between 1996 and 1997 (Table 2; e.g., Fig. 3). Fruits per plant also did not differ between 1996 and 1998, but decreased from 1997 to 1998 in both habitats (Table 2; Fig. 3a). In contrast, seed size did not vary between 1997 and 1998, but was greater in 1998 than in 1996 in slope habitat (Table 2; Fig. 3b).

Seed size was not correlated with fruit crop size within riparian or slope habitats (Table 3).

However, the relationship between seed size and fruit crop size varied between years in slope habitat (Table 3; Fig. 4). Specifically, seed size was negatively correlated with fruit crop size on slopes in 1996 ( $r^2 = -0.61$ ;  $N = 16$ ;  $P$  (multiplied by 3) = 0.048), but not in 1997 ( $r^2 = -0.078$ ;  $N = 36$ ;  $P = 1.00$ ) or 1998 ( $r^2 = 0.028$ ;  $N = 31$ ;  $P = 1.00$ ).

*Fruit size:* Plants in slope habitat produced larger fruits than plants in riparian corridors (net fruit size = fruit volume - seed volume;  $F_{1, 64} = 68.09$ ;  $P < 0.0005$ ). Fruits also differed between habitats in width, length and depth ( $F_{3, 62}$  (approximated with Pillai's Trace) = 29.82;  $P < 0.0005$ ). Average fruit size was positively correlated with seed volume in both riparian ( $F_{1, 29} = 7.58$ ;  $P$  (multiplied by 2) = 0.02) and slope habitat ( $F_{1, 31} = 19.67$ ;  $P$  (multiplied by 2) = 0.0002). Plants in slope and riparian habitat (data for 1999 only) did not differ in the average ratios of pulp-to-seed fresh mass ( $F_{1, 83} = 2.97$ ;  $P = 0.14$ ) or pulp-to-seed dry mass ( $F_{1, 83} = 2.33$ ;  $P = 0.18$ ).

*Seed width/length allometry:* The slope of the regression between log seed length and log seed width was less than 1 for plants in both riparian (slope  $\pm 2$  SE =  $0.45 \pm 0.061$ ;  $df = 91$ ) and slope habitat (slope  $\pm 2$  SE =  $0.53 \pm 0.064$ ;  $df = 91$ ), indicating that seed length increased proportionally faster than seed width with increasing seed size (Fig. 5). The slope of the regression between log fruit length and log fruit width also was less than 1 for plants in both

riparian (slope  $\pm 2$  SE =  $0.74 \pm 0.22$ ; df = 32) and slope habitat (slope  $\pm 2$  SE =  $0.58 \pm 0.27$ ; df = 34).

*Total reproductive biomass:* Total annual seed and fresh fruit mass (i.e., fruit crop size \* estimated seed or fruit mass) were greater for plants in riparian habitat than for similarly-sized plants in slope habitat (Table 1; Fig. 6). Total seed biomass did not differ between 1996 and 1997 or between 1996 and 1998, but decreased between 1997 and 1998 (Table 2).

*Annual variation in precipitation:* Total precipitation in the months preceding fruit ripening (i.e., January through July) did not differ between any two years ( $P \geq 0.40$ ;  $N = 7$  for all tests). In addition, 1996 precipitation from January through July ( $\bar{x} \pm 1$  SD =  $3.83 \pm 2.09$  cm/month) did not differ from 30-year (i.e., 1961-1990) average precipitation levels calculated for the same period ( $\bar{x} = 3.06 \pm 1.06$ ;  $Z = 1.01$ ;  $P = 0.31$ ;  $N = 7$ ). However, 1997 precipitation levels for January through July ( $\bar{x} = 4.09 \pm 1.11$ ) were slightly (although not significantly) greater than average ( $Z = 2.03$ ;  $P = 0.043$ ;  $N = 7$ ), and 1998 precipitation levels ( $\bar{x} = 5.67 \pm 3.79$ ) were slightly greater than average ( $Z = 1.86$ ;  $P = 0.063$ ;  $N = 7$ ; Fig. 7).

## DISCUSSION

Only one previous study of a fleshy-fruited plant has documented patterns of variation in seed traits of plants growing in different environments (Herrera et al. 1994; but see Levey 1990), but differences between environments were not significant. *P. virginiana* reproductive strategies in western Montana, however, clearly differed between slope and riparian habitats. The tradeoff between seed size and number was apparent between but not within these two environments, and

may have resulted from variation in resource limitation or adaptive responses to differing selection pressures.

*Resource Limitation (short versus long-term):*

A short-term response to resource limitation is likely to favor the production of small crops of small seeds, whereas an adaptive response to resource limitation may favor the production of small crops of large seeds. One form of resource limitation, reduced soil moisture, is common for *P. virginiana* in slope habitat and is consistent with the adaptive response hypothesis. Mature *P. virginiana* plants on slopes experienced lower pre-dawn xylem pressure potentials (Fig. 1) and produced smaller crops of larger seeds than plants in riparian areas (Fig. 2). The relatively high levels of abiotic stress in slope habitat may place a premium on traits that enhance seedling establishment, such as large seed size. Seed size has frequently been associated with degree of drought stress, although the correlation may be either positive (Baker 1972; Schimpf 1977; Sultan 1993) or negative (Kramer 1983; Steiner and Grabe 1986; reviewed in Roach and Wulff 1987; Westgate et al. 1989). A negative association between seed size and moisture stress indicates a reduction in the ability of plants to acquire resources necessary for reproduction (Wulff 1986; Venable 1992), but a positive association (e.g., as exhibited by *P. virginiana*) suggests an adaptive response of plants to low-moisture conditions. Large seeds have relatively heavy endocarps, which may better protect the embryo and endosperm within from desiccation or may delay germination until soil moisture levels are adequate for seedling emergence and growth (Baker 1972). In addition, the increase in embryo and endosperm mass in large seeds may enhance nutrient storage capacity and early seedling root growth in dry or nutrient-limited conditions (Baker 1972; Sultan 1996; Milberg and Lamont 1997; Milberg et al. 1998; Lloret et al. 1999).

The additional energy invested into individual fruits and seeds by *P. virginiana* on slopes may occur at the expense of seed number, especially if soil moisture is limited in this habitat (Kaufman 1972; Marshall et al. 1986; Steiner and Grabe 1986; Sultan and Bazzazz 1993a; reviewed in Herrera 1998a; Ho 1992; Stephenson 1992). Several patterns suggest that resources are more limited in slope habitat. First, *P. virginiana* plants on slopes exhibited lower reproductive effort (i.e., total seed and fruit biomass were reduced by 37% and 27%, respectively) compared with plants in riparian areas. Second, the slope environment was the only one in which a fitness tradeoff occurred between seed size and number. These traits were negatively correlated during a relatively dry year (i.e., 1996; Fig. 4a), suggesting that the less optimal growing conditions (at least with respect to soil moisture) may have caused differences in reproductive allocation among plants to outweigh differences in resource acquisition (Bell and Koufopanou 1986; Van Noordwijk and De Jong 1986; Mitchell-Olds 1996a and b).

If seed size and number are directly limited by resource availability, they are likely to vary annually with fluctuating resource levels. In slope habitat (i.e., the habitat with relatively low levels of soil moisture), increased seed size in 1998 (relative to 1996) was associated with slightly greater than average precipitation during the months preceding fruit ripening. Increases in seed size have frequently been associated with increased water availability (Marshall et al. 1986; Roach and Wulff 1987; Castro 1999). However, *P. virginiana* seed size did not increase in 1997 (relative to 1996), another year with slightly greater than average precipitation. In addition, fruit crop size declined in both habitats in 1998 (relative to 1997), causing a decline in total seed mass. The interannual reduction in fruit crop size thus is not likely to have resulted from reductions in soil moisture. However, changes in the timing of occurrence of water or nutrient availability between years may have influenced pollination, early fruit development, or fruit abortion rates (e.g., Mazer et al. 1986; Roach and Wulff 1987; Westgate et al. 1989; Stephenson 1992; Herrera

1998a), and thus influenced fruit abundance or size. Heavy precipitation in 1998, for example, occurred in early spring just after most *P. virginiana* plants began to flower (Parson, pers. obs.; Fig. 7), and may have led to reduced pollination rates or increased mildew infestation on young fruits.

The tendency of *P. virginiana* on slopes to increase seed size rather than seed number with soil moisture suggests that reproductive strategies vary with resource levels, but that large offspring size may play a more important role than number for plants in this habitat. For many plant species, seed size has been found to be phenotypically plastic (e.g., Winn 1985, 1988; Kawano and Nagai 1986; Nagai and Kawano 1986; Schlichting 1986; Wulff 1986; Marshall 1986; Hawke and Maun 1989; Kawano et al. 1989, 1990), resulting largely from indirect effects of the maternal environment (e.g., Mazer 1987; reviewed in Roach and Wulff 1987; Stratton 1989; Schmitt et al. 1992; Schmid and Dolt 1994; Ouborg and Van Treuren 1995; Sultan 1996; Thiede 1998; Castro 1999). The few studies that have examined patterns of variation in seed number and size of fleshy-fruited plants have found substantial variation among years, indicating that maternal effects on seed traits may be large and may minimize the chance of selection on these traits by frugivores (Wheelwright 1993; Jordano 1995a; Alcantara et al. 1997; Herrera 1998a; reviewed in Herrera 1998b). However, the occurrence or extent of plasticity in seed-related traits in response to environmental conditions may allow individuals to maximize offspring fitness in limiting conditions, and in this sense may be adaptive (Haig and Westoby 1988; Winn 1985; Sultan 1987; Schmitt et al. 1992; Sultan and Bazzaz 1993a and b; Sultan 1996; Donohue and Schmitt 1998). Maternal traits may be relatively responsive to natural selection, since additive genetic variation for maternal seed size can be large relative to genetic variation for the size of individual seeds (Antonovics and Schmitt 1986; Mazer 1987; Mojonier 1998).

### *Dispersal Limitation:*

An adaptive response to dispersal limitation may favor the production of large fruit crop sizes, which can result in reduced seed or fruit size. Number of fruits per plant may be the most accurate scale on which frugivores perceive fruit displays (Murray 1987), and number of fruits per raceme may indicate display size on a smaller scale. Thus, the large number of fruits produced at each of these scales in riparian habitat (i.e., the habitat likely to be associated with relatively high dispersal pressure) may represent adaptive responses to increase the chance of consumption by frugivores. In contrast, the production of large seeds rather than large numbers of seeds on slopes suggests that seed dispersal in this environment is relatively unimportant.

Relationships among fruit and seed dimensions did not vary as expected among habitats. Frugivores have been found to select fruits with high pulp-to-seed ratios (e.g., McPherson 1988; Sallabanks 1993), but high ratios were not characteristic of *P. virginiana* plants in riparian habitat (i.e., the habitat likely to be associated with relatively high dispersal pressure). Similar pulp-to-seed ratios in both habitats may indicate that dispersers are abundant relative to fruits and thus do not impose strong selective pressures on fruit traits (Herrera 1981), or that fruits differ in nutritional quality rather than size (Mckey 1975; Howe and Estabrook 1977; Martinez del Rio and Restrepo 1993). Alternatively, the similarity in pulp-to-seed ratios among habitats may have occurred as a result of differences in fruit ripening times. In 1998, only  $74 \pm 40\%$  ( $\bar{x} \pm 1$  SD;  $N = 10$  sites) of plants in riparian sites had fruits that were completely ripe when sampled, while  $92 \pm 26\%$  ( $N = 11$ ) of plants in slope sites had ripe fruits (however, this difference was not significant; KW independent samples test;  $X^2 = 2.28$ ;  $P = 0.13$ ;  $N = 21$ ; habitats were sampled on roughly alternate days from mid to late August). Seed size typically declines with diminishing resources over the season (e.g., Stephenson 1981, 1992; Cavers and Steel 1984; Marshall et al.

1986; Stamp 1990; Wolfe 1995); thus riparian plants that produced fruits late relative to slope plants may have obtained fewer resources to supply all existing seeds with fruit pulp.

Contrary to the allometric hypothesis that seed shape variation is caused primarily by allometric constraints (Herrera 1992), *P. virginiana* seeds in both habitats became increasingly elongated as they increased in width. This change in seed shape with size may be an adaptive response to frugivore gape width limitations. However, seeds from riparian habitat did not exhibit greater change in shape with increasing size than seeds from slopes, despite potentially greater disperser pressure in riparian habitat. Even with little selection for seed dispersability on slopes, pressure to reduce seed and fruit width may be extreme because of the increased likelihood of complete avoidance of fruits by frugivores.

## SUMMARY

Recent interspecific analyses of fruit trait variation have demonstrated large evolutionary constraints on the reproductive phenotypes of fleshy-fruited plants, which may considerably reduce the ability of plants to respond to current dispersal-related selection pressures (Herrera 1986, 1987, 1992; Lee et al. 1991; Janson 1992; Jordano 1995b). However, selection that appears weak at the level of species may in fact be strong at smaller scales (e.g., populations; Thompson 1988). In the present study, substantial environmental variation in reproductive traits within species suggests that these traits are not entirely constrained.

Variation in *P. virginiana* reproductive traits may occur as a result of phenotypic plasticity in response to maternal environmental effects or as a result of specialization (i.e., genetic differentiation) between habitats. The occurrence of plasticity versus specialization as the



predominant source of reproductive variation will depend on the extent to which environmental conditions are correlated across generations (Van Tienderen 1991). Specialization is adaptive when offspring are likely to experience the same selective environments as their parents, whereas plasticity is adaptive when intergenerational environmental correlations are unpredictable (Lynch and Gabriel 1987; Donohue and Schmitt 1998). The degree to which *P. virginiana* seeds are moved between habitats is unknown, but seeds are likely to experience substantial within-habitat heterogeneity (due to soil moisture differences over space and time), particularly on slopes. Thus, plasticity may cause most of the variation in seed size and number within habitats.

In general (with the exception of relatively low pulp-to-seed ratios in riparian habitat), the patterns of variation in *P. virginiana* reproductive traits among environments appear to be adaptive to offspring, if an adaptive phenotype is defined as the one with the highest fitness among all other phenotypes in a given environment (Reeve and Sherman 1993). Large crops of small seeds are produced in the moist environment with potentially high pressure for offspring dispersal, while small crops of large seeds are produced in the dry environment with potentially high pressure for offspring establishment. These patterns occurred consistently over three years, despite the potentially conflicting effects of other unconsidered selective forces (e.g., seed predators, pollinators, herbivores), external factors (e.g., presence of neighboring plants, climatic effects) and fluctuating resource availability on *P. virginiana* fitness. However, the adaptive function of the reproductive strategy on slopes to maternal plants is not clear. Adult plants on slopes produce less fruit and seed biomass than plants in riparian areas, and may ultimately experience increased competition and other density-dependent effects as a result of reduced offspring dispersal. Thus, the consistent production of relatively few, large seeds on slopes is likely to result from high selective pressure on offspring fitness.

To understand the fitness implications of variation in offspring size and number, the effects of these traits must be analyzed during the subsequent stages of offspring recruitment in the offsprings' own environments. Ideally, quantitative genetic analyses of maternal inheritance should be used to determine the extent of maternal versus Mendelian inheritance in fruit and seed traits, and ultimately the overall response to selection (i.e., heritability; Wheelwright 1993; Theide 1998; unfortunately, these analyses may be nearly impossible to perform on long-lived woody plants). The present study thus provides a starting point for further investigation into the extent and consequences of environmental variation in the reproductive phenotypes of animal-dispersed plants.

## LITERATURE CITED

- Alcantara, J. M., P. J. Rey, F. Valeara, A. M. Sanchez-Lafuente and J. E. Gutierrez. 1997. Habitat alteration and plant intra-specific competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. *Oikos* 79: 291-300.
- Antonovics, J. and D. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Ann. Rev. Ecol. Syst.* 11: 411-452.
- Antonovics, J. and J. Schmitt. 1986. Paternal and maternal effects on propagule size in *Anthoxanthum odoratum*. *Oecologia* 69: 277-282.
- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997-1010.
- Baker, K. B., A. J. Richards, and M Tremayne. 1994. Fitness constraints on flower number, seed number and seed size in the dimorphic species *Primula farinosa* L. and *Armeria maritima* (Miller) Willd. *New Phytol.* 128: 563-570.
- Barot, S., J. Gignoux and J. C. Menaut. 1999. Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. *Oikos* 86: 320-330.
- Bell, G. and V. Koufopanou. 1986. The cost of reproduction. *Oxford Surveys in Evol. Biol.* 3: 83-131.
- Capinera, J. L. 1979. Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* 114: 350-361.
- Castro, J. 1999. Seed mass versus seedling performance in Scots pine: a maternally dependent trait. *New Phytol.* 144: 153-161.

- Cavers, P. B. and M. G. Steel. 1984. Patterns of change in seed weight over time on individual plants. *Am. Nat.* 124: 324-335.
- Christie, B. R. and R. R. Kalton. 1960. Recurrent selection for seed weight in brome grass *Bromus inermis* Lyess. *Agronomy Journal* 52: 575-578.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In*: Den Boer, P. J. and G. Gradwell (eds). Dynamics of populations. PUDOC, Wageningen, pp. 298-312.
- Debussche, M., and P. Isenmann. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* 56: 327-338.
- Donohue, K. and J. Schmitt. 1998. Maternal environmental effects in plants: Adaptive plasticity? *In*: Mousseau, T. A. and C. W. Fox (eds.). Maternal effects as adaptations. Oxford Univ. Press, New York.
- Fenner, M. 1985. Seed ecology. Chapman and Hall, New York.
- Foster, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Bot. Rev.* 52: 260-299.
- Fox, G. A. 1990. Drought and the evolution of flowering time in desert annuals. *Am. J. Bot.* 77: 1508-1518.
- Galen, C. and H. G. Weger. 1986. Reevaluating the significance of correlations between seed number and size: Evidence from a natural population of the lily, *Clintonia borealis*. *Am J. Bot.* 73: 346-352.
- Ganeshaiah, K. N and R. Uma-Shaanker. 1991. Seed size optimization in a wind dispersed tree *Butea monosperma*: A trade-off between seedling establishment and pod dispersal efficiency. *Oikos* 60: 3-6.
- Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J. Ecol.* 72: 369-387.

- Haig, D. and M. Westoby. 1988. Inclusive fitness, seed resources, and maternal care. *In*: Lovett-Doust, J. and L. Lovett-Doust (eds.), Plant reproductive ecology: patterns and strategies. Oxford University Press, New York.
- Hammond, D. S. and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. *Ecology* 76: 2544-2561.
- Hansen, P. 1989. Source/sink effects in fruits; an evaluation of various elements. *In*: Wright, C. J. (ed.), Manipulation of fruiting. Butterworths, London.
- Hawke, M. A and M. A. Maun. 1989. Intrapopulation variation in reproduction and seed mass of a beach annual; *Cakile edentula* var. *lacustris*. *J. Coastal Res.* 5: 103-112.
- Herrera, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36: 51-58.
- Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. *In*: Estrada, A. and T. H. Fleming (eds.), Frugivores and seed dispersal. Junk, Dordrecht.
- Herrera, C. M. 1987. Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecol. Monogr.* 57: 305-331.
- Herrera, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 140: 421-446.
- Herrera, C. M. 1998a. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr.* 68: 511-538.
- Herrera, C. M. 1998b. Population-level estimates of interannual variability in seed production: what do they actually tell us? *Oikos* 82: 612-616.
- Herrera, C. M., P. Jordano, L. Lopez-Soria and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.* 64: 315-344.

- Ho, L. C. Fruit growth and sink strength. 1992. Fruit growth and sink strength. *In*: Marshall, C. and J. Grace (eds.). Fruit and seed production: aspects of development, environmental physiology and ecology. Cambridge University Press, Cambridge, UK.
- Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320-329.
- Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecol.* 61: 944-959.
- Howe, H. F. 1990. Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. *J. Tropic. Ecol.* 6: 259-280.
- Howe, H. F. and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111: 817-832.
- Howe, H. F. and W. M. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347-351.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781-791.
- Janson, C. H. 1992. Measuring evolutionary constraints: a Markov model for phylogenetic transitions among seed dispersal syndromes. *Evolution* 46: 136-158.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 521-528.
- Jordano, P. 1987. Frugivory, external morphology and digestive system in Mediterranean sylviid warblers *Sylvia* spp. *Ibis* 129: 175-189.
- Jordano, P. 1995a. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* 76: 2627-2639.
- Jordano, P. 1995b. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am Nat.* 145: 163-191.

- Kang, H. and R. B. Primack. 1991. Temporal variation of flower and fruit size in relation to seed yield in celandine poppy (*Chelidonium majus*: Papaveraceae). *Am. J. Bot.* 78: 711-722.
- Kaspari, M. 1993. Removal of seeds from neotropical frugivore droppings: ant responses to seed number. *Oecologia* 95: 81-88.
- Kaufman, M. R. 1972. Water deficits and reproductive growth. In Kozlowski, T. T. (ed.). Water deficits and plant growth, vol. III. Plant responses and control of water balance. Academic Press, New York.
- Kawano, S., T. Hara, A. Hiratsuka, K. Matsuo and I. Hirota. 1990. Reproductive biology of an amphicarpic annual, *Polygonum thunbergii* (Polygonaceae): Spatio-temporal changes in growth, structure and reproductive components of a population over an environmental gradient. *Pl. Spec. Biol.* 5: 97-120
- Kawano, S. and Y. Nagai. 1986. Regulatory mechanisms of reproductive efforts in plants: I. Plasticity in reproductive energy allocation and propagule output of *Helianthus annuus* L. (Compositae) cultivated at varying densities and nitrogen levels. *Pl. Spec. Biol.* 1: 1-18.
- Kawano, S., H. Takasu and T. Oritani. 1989. Regulatory mechanisms of reproductive effort in plants. III. Plasticity in reproductive energy allocation and propagule output of two grass species *Oryza sativa* cv. *Akihikari* and *Coix ma-yuen* cultivated at varying densities and nitrogen levels, and the evolutionary-ecological implications. *Pl. Spec. Biol.* 4: 75-99.
- Klinkhamer, P. G. L. and T. J. De Jong. 1987. Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytologist* 106: 773-784.
- Kramer, P. J. 1983. Water relations of plants. New York, Academic Press.
- Lee, W. G., P. J. Grubb and J. B. Wilson. 1991. Patterns of resource allocation in fleshy fruits of nine European tall-shrub species. *Oikos* 61: 307-315.

- Levey, D. J. 1986. Methods of seed processing by birds and seed deposition patterns. *In*: Estrada, A. and T. H. Fleming (eds.). *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129: 471-485.
- Levey, D. J. 1990. Habitat-dependent fruiting behavior of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *J. Trop. Ecol.* 6: 409-420.
- Lloret, F., C. Casanovas and J. Penuelas. 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Funct. Ecol.* 13: 210-216.
- Lynch, M. and W. Gabriel. 1987. Environmental tolerance. *Am. Nat.* 129: 283-303.
- Lyons, E. E. and J. Antonovics. 1991. Breeding system evolution in *Leavenworthia crassa* (Cruciferae). *Am. J. Bot.* 78: 270-287.
- Marshall, D. L. 1986. Effect of seed size on seedlings success in three species of *Sesbania* (Fabaceae). *Am. J. Bot.* 73: 457-464.
- Marshall, D. L., D. A. Levin and N. L. Fowler. 1986. Plasticity of yield components in response to stress in *Sesbania macrocarpa* and *Sesbania vesicaria* (Leguminosae). *Am. Nat.* 127: 508-521.
- Martinez del Rio, C. and C. Restrepo. 1993. Ecological and behavioral consequences of digestion in frugivorous animals. *Vegetatio* 107/108: 205-216.
- Mazer, S. J. 1987. Quantitative genetics of life history and fitness components in *Raphanus raphanistrum*: ecological and evolutionary consequences of seed-weight variation. *Am. Nat.* 130: 891-914.



- Mazer, S. J., A. A. Snow and M. L. Stanton. 1986. Fertilization dynamics and parental effects upon fruit development in *Raphanus raphanistrum*: Consequences for seed size variation. *Am. J. Bot.* 73: 500-511.
- Mazer, S. J. and N. T. Wheelwright. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evol. Ecol.* 7: 556-575.
- McGinley, M. A. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.* 130: 370-398.
- McGinley, M. A. 1989. Within and among plant variation in seed mass and pappus size in *Tragopogon dubius*. *Can. J. Bot.* 67: 1298-1304.
- Mckey, D. 1975. The ecology of coevolved dispersal systems. *In*: Gilbert, L. E. and P. H. Raven (eds.). *Coevolution of animals and plants*. Univ. of Texas Press, Austin.
- McPherson, J. M. 1988. Preferences of cedar waxwings in the laboratory for fruit species, color and size: a comparison with field observations. *Anim. Behav.* 36: 961-969.
- Meyer, G. A. and M. C. Witmer. 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *Am. Midl. Nat.* 140: 129-139.
- Michaels, H. J., B. Benner, A. P. Hartgerink, T. D. Lee, S. Rice, M. Willson and R. I. Bertin. 1989. Seed size variation: magnitude, distribution, and ecological correlates. *Evol. Ecol.* 2(2): 157-166.
- Milberg, P. and B. B. Lamont. 1997. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytol.* 137: 665-672.
- Milberg, P. M. A. Perez-Fernandez and B. B. Lamont 1998. Seedling growth response to added nutrients depends on seed size in three woody genera. *J. Ecol.* 86: 624-632.
- Mitchell-Olds, T. 1996a. Genetic constraints on life history evolution: quantitative trait loci influencing growth and flowering in *Arabidopsis thaliana*. *Evolution* 50: 140-145.

- Mitchell-Olds, T. 1996b. Pleiotropy causes long-term genetic constraints on life history evolution in *Brassica rapa*. *Evolution* 50: 1849-1858.
- Mojonnier, L. 1998. Natural selection on two seed-size traits in the common morning glory *Ipomoea purpurea* (Convolvulaceae): patterns and evolutionary consequences. *Am. Nat.* 152: 188-203.
- Morse, D. H. and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. *Oecologia* 67: 372-379.
- Murray, K. G. 1987. Selection for optimal fruit crop size in bird-dispersed plants. *Am. Nat.* 129: 18-31.
- Nagai, Y. and S. Kawano. 1986. Regulatory mechanisms of reproductive effort in plants. II. Plasticity in reproductive energy allocation and propagule output of *Glycine max* Merr. (Leguminosae) cultivated at varying densities and nitrogen levels. *Pl. Spec. Biol.* 1: 181-194.
- Ogden, J. 1974. The reproductive strategy of higher plants. II. The reproductive strategy of *Tussilago farfara* L. *J. Ecol.* 62: 291-324.
- Ouborg, N. J and R. Van-Treuren. 1995. Variation in fitness-related characters among small and large populations of *Salvia pratensis*. *J. Ecol.* 83: 369-380
- Platt, W. J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). *Oecologia* 22: 399-409.
- Roach, D. A. and R. D. Wulff. 1987. Maternal effects in plants. *Ann. Rev. Ecol. Syst.* 18: 209-235.
- Roff, D. R. 1992. The evolution of life histories. Chapman and Hall, New York.
- Ridley, H. N. 1930. The dispersal of plants throughout the world. Reeve, Ashford, England.
- Sallabanks, R. S. 1992. Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn. *Crataegus monogyna* (Rosaceae). *Oecologia* 91: 296-304.

- Sallabanks, R. S. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326-1336.
- Schimpf, D. 1977. Seed weight of *Amaranthus retroflexus* in relation to moisture and length of growing season. *Ecol.* 58: 450-453.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annu. Rev. Ecol. Syst.* 17: 667-693.
- Schmid, B. and C. Dolt. 1994. Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima* L. *Evolution* 48: 1525-1549.
- Schmitt, J., J. Niles, and R. D. Wulff. 1992. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *Am. Nat.* 139: 451-466.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82: 399-409.
- Smith, C. C. and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108: 499-506.
- Stamp, N. E. 1990. Production and effect of seed size in a grassland annual (*Erodium brachycarpum*, Geraniaceae). *Am. J. Bot.* 77: 874-882.
- Stanton, M. L. 1984. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *Am. J. Bot.* 71: 1090-1098.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* 51: 3-49.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.
- Steiner, J. J and D. F. Grabe. 1986. Sheep grazing effects on subterranean clover (*Trifolium subterraneum*) development and seed production in western Oregon (USA). *Crop Science* 26: 367-372.
- Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Ann. Rev. Ecol. Syst.* 12: 253-279.

- Stephenson, A. G. 1992. The regulation of maternal investment in plants. *In*: Marshall, C. and J. Grace (eds.). *Fruit and seed production: aspects of development, environmental physiology and ecology*. Cambridge University Press, Cambridge, UK.
- Stratton, D. J. 1989. Competition prolongs expression of maternal effects in seedlings of *Erigeron annuus* (Asteraceae). *Am. J. Bot.* 76: 1646-1653.
- Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* 21: 127-176.
- Sultan, S. E. 1993. Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution* 47: 1032-1049.
- Sultan, S. E. 1996. Phenotypic plasticity for offspring traits in *Polygonum Persicaria*. *Ecology* 77: 1791-1807.
- Sultan, S. E. and F. A. Bazzaz. 1993a. Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution* 47: 1032-1049.
- Theide, D. A. 1998. Maternal inheritance and its effect on adaptive evolution: a quantitative genetic analysis of maternal effects in a natural plant population. *Evolution* 52: 998-1015.
- Thompson, J. N. 1988. Variation in interspecific interactions. *Ann. Rev. Ecol. Syst.* 19: 65-87.
- Van Noordwijk, A. J. and G. De Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128: 137-142.
- Van Tienderen, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution*: 45: 1317-1331.
- Venable, D. L. 1992. Size-number trade-offs and the variation of seed size with plant resource status. *Am. Nat.* 140: 287-304.

- Venable, D. L. and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131: 360-384.
- Waller, D. M. 1982. Factors influencing seed weight in *Impatiens capensis* (Balsaminaceae). *Am. J. Bot.* 69: 1470-1475.
- Westgate, M. E., J. R. Schussler, D. C. Reicosky and M. L. Brenner. 1989. Effect of water deficits on seed development in soybean: II. Conservation of seed growth rate. *Plant Physiology* 91: 980-985.
- Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808-818.
- Wheelwright, N. T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Vegetatio* 107/108: 163-174.
- Willson, M. F. 1983. Plant reproductive ecology. John Wiley and Sons, New York.
- Willson, M. F. and P. W. Price. 1980. Resource limitation of fruit and seed production in some *Asclepias* species. *Can. J. Bot.* 58: 2229-2233.
- Winn, A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *J. Ecol.* 73: 831-840.
- Winn, A. A. 1988. Ecological and evolutionary consequences of seed size in *Prunella vulgaris*. *Ecology* 69: 1537-1544.
- Wolfe, L. M. 1995. The genetics and ecology of seed size variation in a biennial plant, *Hydrophyllum appendiculatum* (Hydrophyllaceae). *Oecologia* 101: 343-352.
- Wulff, R. D. 1986. Seed size variation in *Desmodium Paniculatum*: I. Factors affecting seed size. *J. Ecol.* 74: 87-97.

**Table 1.** General Factorial ANCOVA results for habitat, year and canopy volume effects (two-way interactions were not significant) on *P. virginiana* seed number, size and total seed or fruit mass, 1996-1998.

Dependent Variable	Factors / Covariate	F	df <sup>a</sup>	p <sup>b,c</sup>
<b>Fruits / plant</b>	<b>Habitat</b>	57.69	1, 172	<b>&lt;0.0005</b>
	<b>Year</b>	7.34	2, 172	<b>0.001</b>
<b>Fruits / raceme<sup>d</sup></b>	<b>Canopy Volume</b>	30.55	1, 172	<b>&lt;0.0005</b>
	<b>Habitat</b>	95.23	1, 103	<b>&lt;0.0005</b>
	<b>Year</b>	0.035	1, 103	0.85
	<b>Canopy Volume</b>	0.21	1, 103	0.65
<b>Seed Vol. / plant</b>	<b>Habitat</b>	64.65	1, 177	<b>&lt;0.0005</b>
	<b>Year</b>	1.80	2, 177	0.17
	<b>Canopy Volume</b>	13.65	1, 177	<b>&lt;0.0005</b>
	<b>Habitat</b>	40.28	1, 161	<b>&lt;0.0005</b>
<b>Total Seed Mass / plant</b>	<b>Year</b>	2.10	2, 161	0.13
	<b>Canopy Volume</b>	29.17	1, 161	<b>&lt;0.0005</b>
	<b>Habitat</b>	11.24	1, 64	<b>0.001</b>
	<b>Year</b>	6.67	1, 64	<b>0.012</b>
<b>Total Fruit Mass / plant<sup>e</sup></b>	<b>Canopy Volume</b>	1.63	1, 76	0.21

<sup>a</sup> Group and error df, respectively

<sup>b</sup> Tests significant at  $\alpha = 0.05$  indicated in bold

<sup>c</sup> Error variances were not equal for fruits per plant ( $F = 4.79$ ;  $df = 5, 171$ ;  $P \leq 0.0005$ ) or fruits per raceme ( $F = 8.66$ ;  $df = 3, 103$ ;  $P \leq 0.0005$ )

<sup>d</sup> Data for 1996 and 1997 only

<sup>e</sup> Data for 1997 and 1998 only

**Table 2.** Paired t-test results for between-year differences in *P. virginiana* seed number, size and total seed mass, 1996-1998.

Between Years	Dependent Variable	Riparian			Slope		
		<i>t</i>	df	P <sup>a</sup>	<i>t</i>	df	P
1996 & 1997	Fruits/plant	0.80	6	1.00	1.09	15	1.00
	Fruits/raceme	-0.035	12	1.00	0.61	20	1.00
	Seed volume/plant	-0.46	16	1.00	-2.06	20	0.32
	Total seed mass/plant	0.73	6	1.00	0.44	15	1.00
1997 & 1998	<b>Fruits/plant</b>	<b>4.54</b>	<b>32</b>	<b>0.0005</b>	<b>4.62</b>	<b>35</b>	<b>0.0003</b>
	Seed volume/plant	1.05	30	1.00	1.46	26	0.96
	<b>Total seed mass/plant</b>	<b>4.74</b>	<b>31</b>	<b>0.0003</b>	<b>4.54</b>	<b>35</b>	<b>0.0004</b>
1996 & 1998	Fruits/plant	1.65	6	0.90	2.29	15	0.22
	<b>Seed volume/plant</b>	<b>-0.054</b>	15	1.00	<b>-3.85</b>	<b>14</b>	<b>0.012</b>
	Total seed mass/plant	1.57	6	1.00	1.69	15	0.66

<sup>a</sup> Tests significant at  $\alpha = 0.05$  indicated in bold (p-values have been multiplied by 6 for fruits/plant, seed volume/plant and total seed mass/plant, and multiplied by 2 for fruits/raceme)

**Table 3.** General Factorial ANCOVA results for effects of year, fruit crop size (i.e., fruits per plant) and canopy volume (two-way interactions included only if significant) on seed size in riparian and slope habitat, 1996-1998.

Factor / covariates	Habitat				
	Riparian		Slope		
	F	df <sup>a</sup>	P <sup>b</sup>	F	df <sup>a</sup> P <sup>b,c</sup>
Year	0.41	2, 77	1.00	3.07	2, 76 0.10
Crop Size	0.78	1, 77	0.76	0.10	1, 76 1.00
<b>Canopy Volume</b>	<b>8.45</b>	<b>1, 77</b>	<b>0.01</b>	<b>0.095</b>	<b>1, 76 1.00</b>
<b>Year*Crop Size<sup>d</sup></b>	---	---	---	<b>4.47</b>	<b>2, 76 0.03</b>

<sup>a</sup> Group and error df, respectively

<sup>b</sup> Tests significant at  $\alpha = 0.05$  indicated in bold (p-values have been multiplied by 2)

<sup>c</sup> Error variances were not equal (F = 3.22; df = 2, 80; P = 0.045)

<sup>d</sup> Interaction was not included in the final model for riparian habitat since it was not significant



## FIGURE LEGENDS

**Figure 1.** Predawn xylem pressure potentials (PDXPP) of adult *P. virginiana* plants in riparian and slope habitats. August 1998.

**Figure 2.** Estimated marginal means for (a) fruits per plant and (b) average seed size ( $\text{mm}^3$ ) of *P. virginiana* plants in riparian and slope habitats, 1996-1998. Effects of year and canopy volume have been removed.

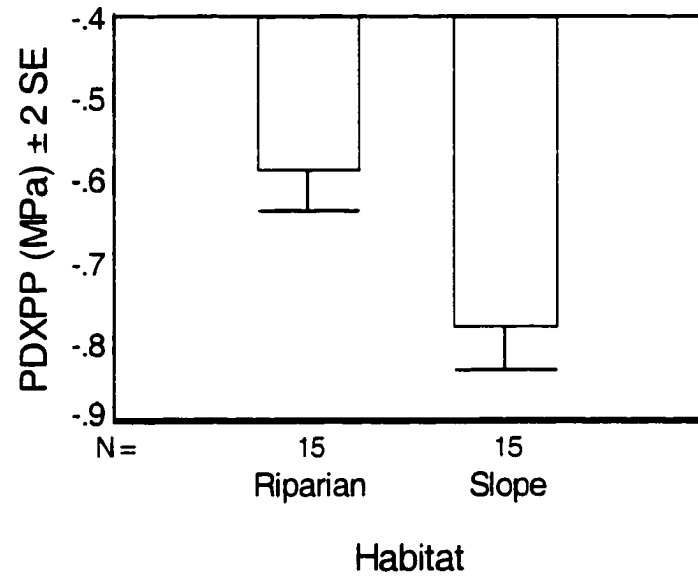
**Figure 3.** Difference in (a) fruits per plant and (b) average seed size ( $\text{mm}^3$ ) of *P. virginiana* plants between pairwise combinations of years; significant differences from zero are indicated by asterisks ( $\alpha = 0.05$ ; p-values multiplied by 2).

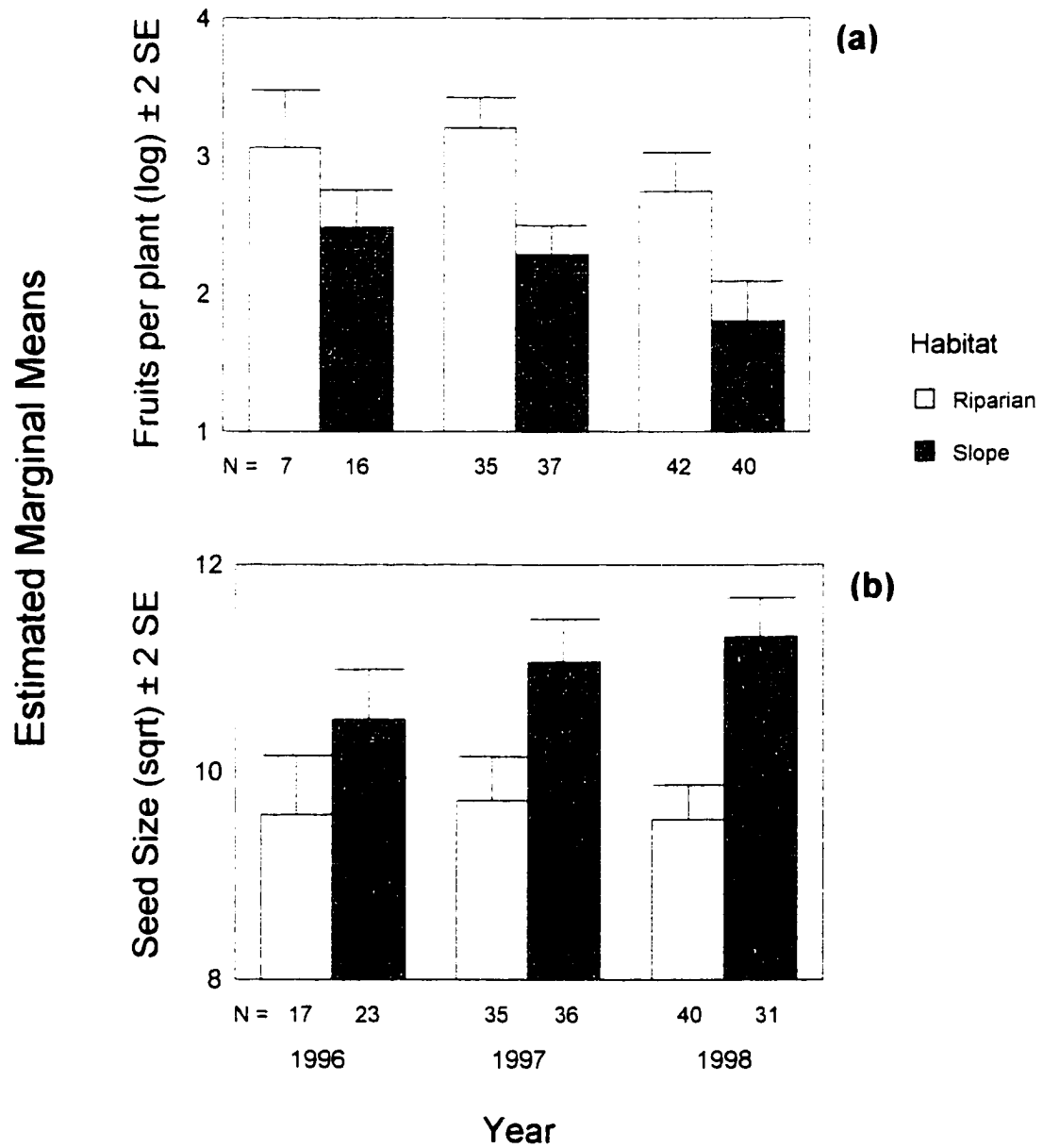
**Figure 4.** Partial regression plots of the association between fruits per plant and seed size ( $\text{mm}^3$ ) of *P. virginiana* plants in slope habitat in (a) 1996, (b) 1997 and (c) 1998. Effects of canopy volume have been removed.

**Figure 5.** Log seed width (mm) versus length (mm) for *P. virginiana* plants in riparian and slope habitat, 1996 – 1998.

**Figure 6.** Estimated marginal means for (a) total seed mass (i.e., fruit crop size\*estimated seed mass) of *P. virginiana* plants, 1996 - 1998, and (b) total fresh fruit mass (i.e., fruit crop size\*estimated fruit mass) of *P. virginiana* plants, 1996 - 1998. Effects of year and canopy volume have been removed.

**Figure 7.** Precipitation in Missoula, MT in the months preceding fruit ripening (30-year average and 1996 – 1998).

**FIGURE 1**



**FIGURE 2**

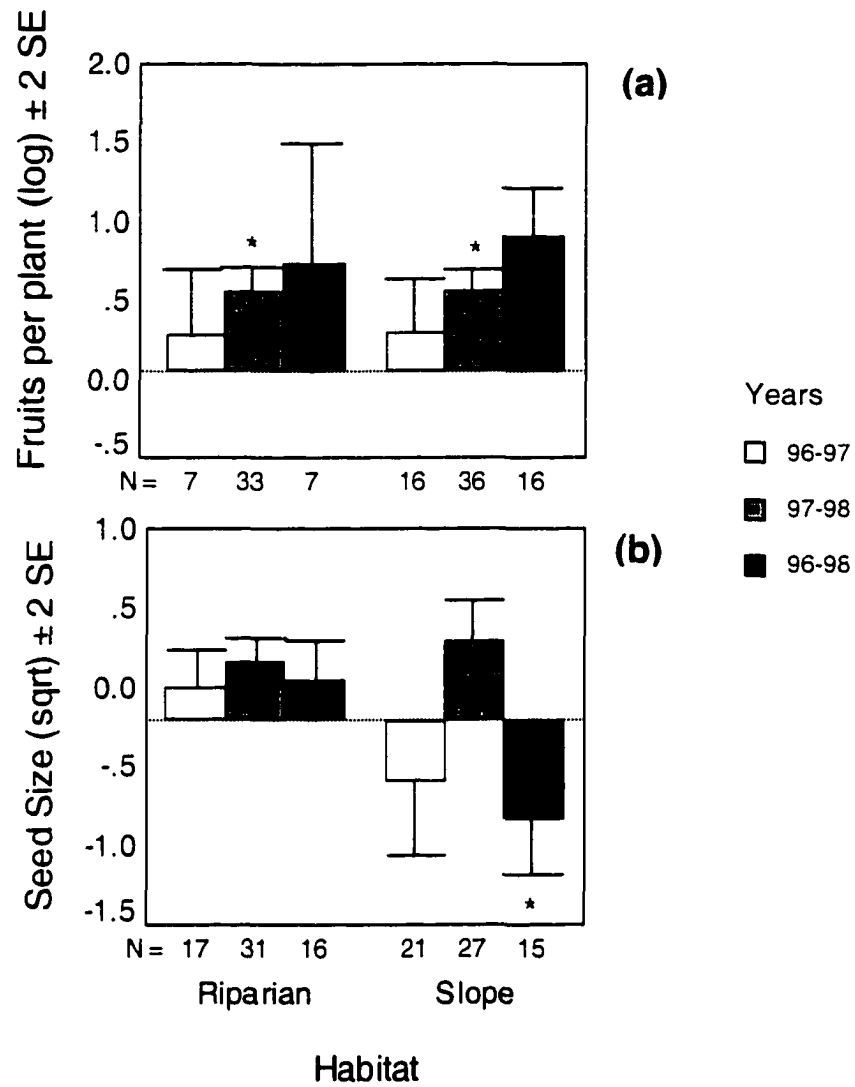
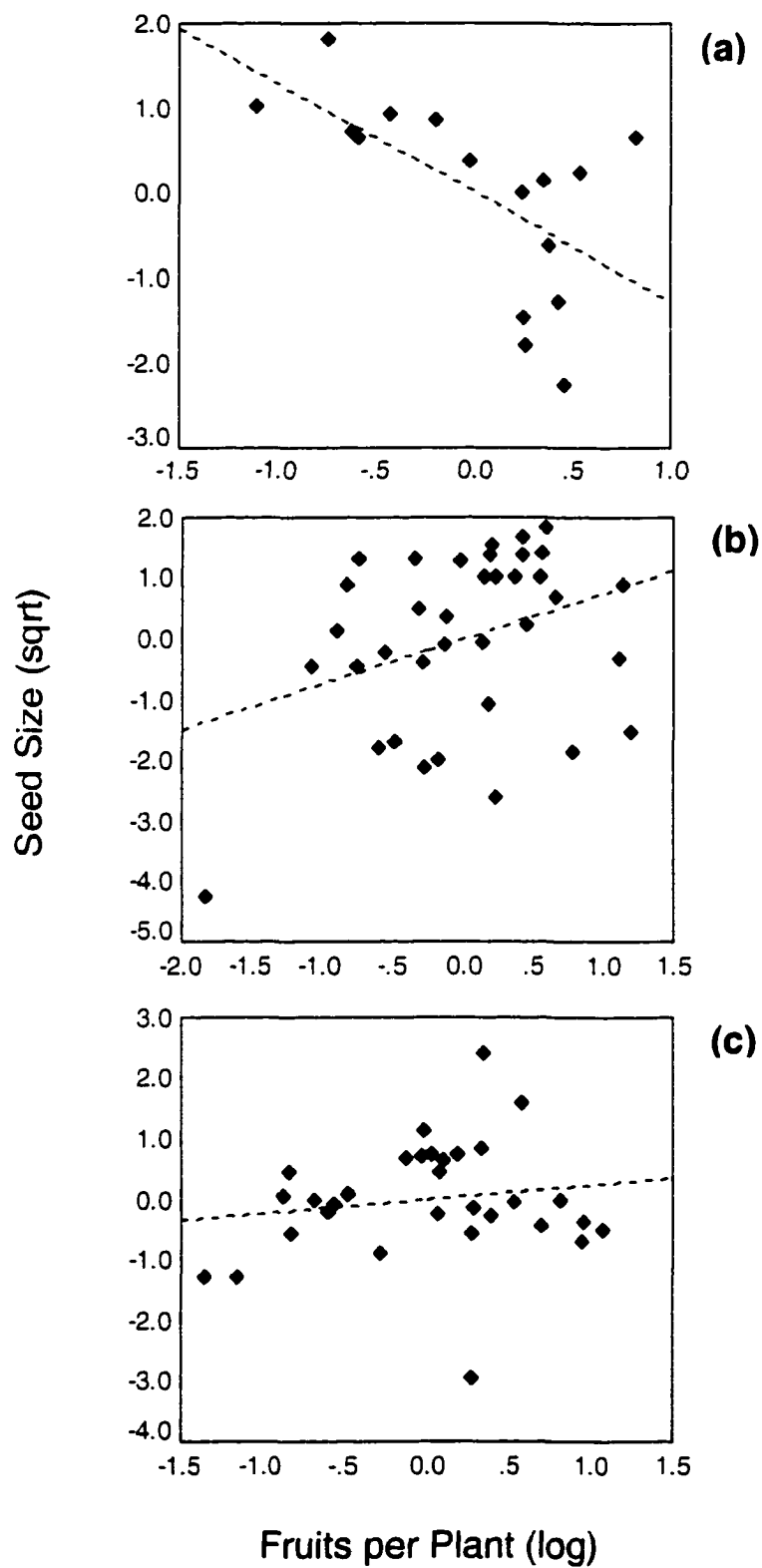
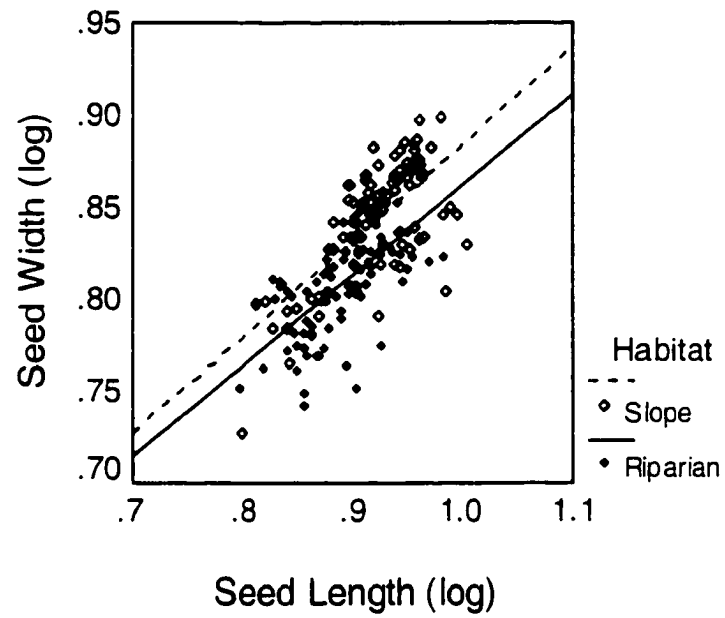
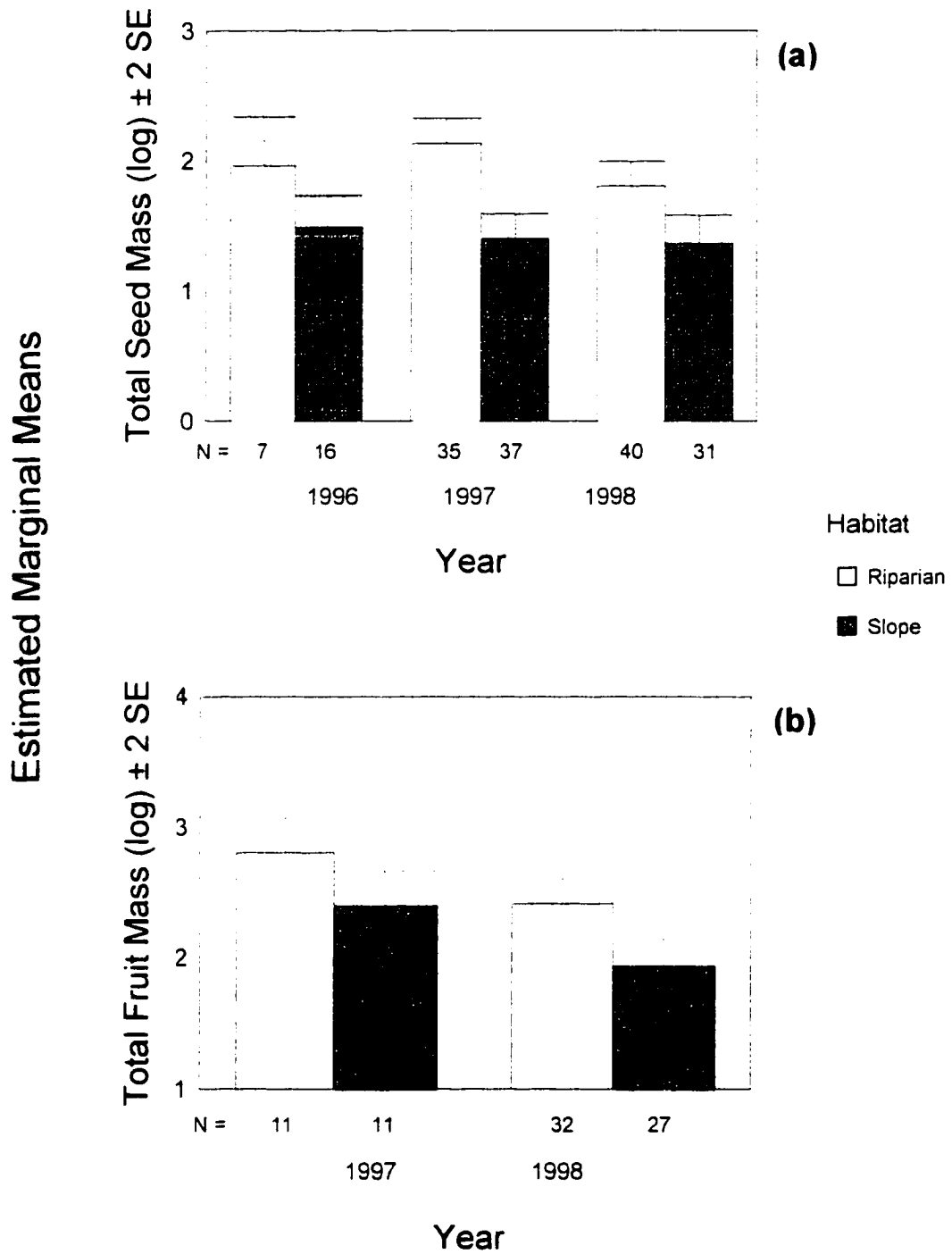


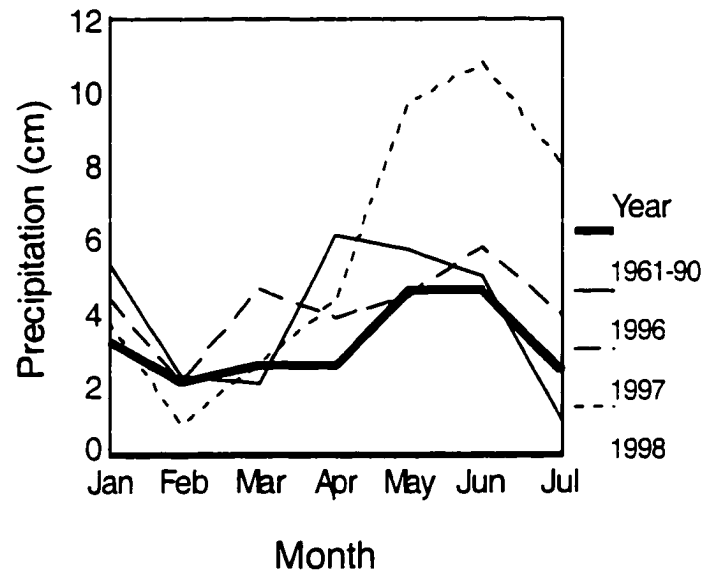
FIGURE 3

**FIGURE 4**

**FIGURE 5**



**FIGURE 6**

**FIGURE 7**



## **CHAPTER 2**

### **Seed Size, Number and Habitat of a Fleshy-Fruited Plant: Consequences for Seed Dispersal.**

## INTRODUCTION

Plant reproductive traits such as seed number and size can indirectly determine patterns of offspring establishment by their effect on patterns of seed dispersal (i.e., the quantity and quality of dispersed seeds; e.g., Willson 1993; Schupp 1995). The link between plant reproduction and offspring establishment may be connected by determining the role of reproductive traits in dispersal, and subsequently the influence of dispersal patterns on offspring establishment. However, studies that attempt to provide such a link are rare (Howe 1990 and previous papers; Augspurger and Kitajima 1992; Herrera et al. 1994).

Seed size and number stand out from other reproductive traits in their ability to influence both seed dispersal patterns and seedling establishment. Maternal plants may experience selection for the production of large numbers of small seeds, since large seed crops increase maternal fecundity and both large crops and small seed sizes can increase seed dispersal (e.g., Baker 1972; Howe 1980; Howe and Richter 1982; Morse and Schmitt 1985; Sallabanks 1992; Jordano 1995). Individual seeds can benefit from such dispersal, but may also benefit from large size during offspring establishment (e.g., Howe et al. 1985; Foster 1986; Winn 1988; Gross and Smith 1991; Mazer and Wolfe 1998). If a resource allocation tradeoff between seed size and number exists, these traits may be selected upon in opposite directions for maternal and offspring generations (Donohue 1998; Donohue and Schmitt 1998; Donohue 1999). Examination of the consequences of seed size and number variation throughout offspring recruitment thus is critical to understand the importance of these traits for both maternal and offspring fitness. Intraspecific variation in seed size and number is common (e.g., Willson and Price 1980; Marshall 1986; Wulff 1986; McGinley 1989; Sultan and Bazzaz 1993; Baker et al. 1994), but the combined effect of these traits on dispersal and establishment has not been studied.

Dispersal may be especially important for animal-dispersed plants because animals can exert selective pressures both through their foraging preferences and subsequent dispersal patterns (e.g., McKey 1975; Howe and Estabrook 1977; Jordano 1995). However, dispersal systems may vary in space and time, such that patterns of frugivore abundance, frugivore preferences, seed deposition or offspring establishment are rarely consistent (e.g., Herrera 1985, 1998; Horvitz and Schemske 1986; Schupp 1988a; Whelan et al. 1991; Sallabanks 1993; Willson and Whelan 1990, 1993; Guitan et al. 1992; Jordano 1993; Notman et al. 1996). As a result, selection pressures imposed by animal dispersers may not have strong net effects on the dispersal process.

One factor that may contribute to variation in dispersal is spatial environmental heterogeneity. Plants in such environments may be subject to different assemblages of frugivores or to differences in the post-foraging patch or perch choices of frugivores (e.g., Denslow and Moermond 1982; Piper 1986; Bronstein and Hoffman 1987; Malmborg and Willson 1988; Guitan et al. 1992; reviewed in Schupp and Fuentes 1995). Differences in frugivore activities in turn can result in different patterns of seed deposition within species (e.g., McDonnell and Stiles 1983; Hoppes 1988; Willson and Crome 1989; Chavez-Ramirez and Slack 1994; Herrera et al. 1994). This variation in dispersal patterns is further complicated by spatial variation in biotic and abiotic seed or seedling mortality factors (e.g., Webb and Willson 1985; Schupp 1988b; Gill and Marks 1991; Myster and Pickett 1993; Horvitz and Schemske 1994; Russell and Schupp 1998). Thus, local investigations of dispersal systems are necessary to obtain an accurate picture of the consequences of dispersal (Schupp and Fuentes 1995).

This study examines the relationship between seed size, number, dispersal and offspring recruitment of common chokecherry (*Prunus virginiana*) in spatially-variable local environments. This fleshy-fruited, primarily bird-dispersed tree grows in western Montana in two distinct habitats, where it produces either large crops of small seeds (riparian habitat), or small crops of

large seeds (slope habitat; Ch. 1). The direct effect of *P. virginiana* seed size, number and habitat on dispersal must be determined to understand the indirect consequences of these factors for seedling establishment (see Ch. 3 for this subsequent study). Here, I consider three primary hypotheses for possible dispersal-related causes of the general pattern of reproductive variation between habitats: **(1) Fruit Consumption:** Between-habitat variation in seed size and number may reflect selection for dispersal by frugivores, assuming that plants compete for frugivores. If frugivores prefer *P. virginiana* plants with large crops of small seeds, then they should use such plants out of proportion to their availability. This pattern of use with respect to crop size is likely to be apparent in riparian but not slope habitat. Within plants, frugivores may make foraging decisions based on seed size, but no *a priori* predictions were made about the net effect of frugivore preferences for seed size. Preferences for small and large seeds or fruits have been documented for other fleshy-fruited plant species (Howe and Van de Kerckhove 1981; Wheelwright 1985; McPherson 1988; Sallabanks 1993; Wheelwright 1993; Jordano 1995).

**(2) Seed Predation:** Plant reproductive strategies also may reflect negative selection pressures imposed by pre-dispersal seed predators (reviewed by Herrera 1986; pressures imposed by post-dispersal predators will be examined in Ch. 3). If large fruit crops are produced by riparian *P. virginiana* to satiate vertebrate seed predators, then levels of seed predation should be higher in riparian habitat than on slopes, and riparian plants with large crops should have lower proportional seed predation than plants with small crops (Janzen 1976, Silvertown 1980).

**(3) Seed Dispersal Patterns:** If the production of large crops of small seeds by riparian plants is an adaptive response to enhance seed dispersal, then *P. virginiana* seeds should be deposited at greater distances from adult conspecifics in riparian habitat than on slopes. However, external factors associated with habitats also may influence seed dispersal patterns. If post-foraging perch sites are relatively abundant along riparian corridors, then frugivores in riparian habitat should fly

along rather than away from corridors after foraging and are most likely to deposit seeds in these areas.

## STUDY AREA AND METHODS

All measurements of *P. virginiana* seed dispersal patterns were conducted in the foothills of the Rocky Mountains of western Montana (~1000m elevation) from 1996 - 1998. *P. virginiana* is a shrubby tree that produces fleshy fruits with hardened endocarps (i.e., inner walls) that enclose single seeds until germination. The fruits are particularly attractive to avian frugivores, which consume the fruit pulp and excrete, regurgitate or drop the seeds. Primary frugivores on *P. virginiana* in western Montana are *Bombycilla cedrorum* and *Turdus migratorius* (Parson, pers. obs.). These two species may differ in preferred size of fruits or seeds, length of time to process seeds and in post-foraging behavior (McPherson 1988; Sallabanks 1993; Meyer and Witmer 1998; Chavez-Ramirez and Slack 1994). Although the preferences and seed deposition patterns of the two species were combined for this study, these cumulative effects ultimately will influence plant reproductive strategies. Both species are likely to have a positive effect on *P. virginiana* seed germination simply by removing fruit pulp from the seeds (Meyer and Witmer 1998). Thus, these frugivores may impose net selection pressure on the size and number of seeds produced. In western Montana, *P. virginiana* typically occurs in two distinct habitat types: scattered in isolated clumps on south to west-facing slopes (generally on exposed, rocky faces) and as part of a continuous band of vegetation on the edges of riparian corridors (Parson, unpubl. data). In the relatively xeric slope habitat, *P. virginiana* produces small crops of large fruits and seeds, while in the more mesic riparian habitat *P. virginiana* produces large crops of small fruits and seeds (Ch. 1). Because of the variation in reproductive strategies and environmental

conditions between habitats, *P. virginiana* individuals are likely to experience markedly different selection pressures for seed dispersal and offspring establishment.

#### *Fruit Consumption and Seed Predation:*

The relationship between frugivore preferences and plant, fruit crop and seed characteristics was determined for 33 adult *P. virginiana* plants in 1997 and for 34 plants in 1998 (24 of these plants were sampled in both years). Approximately half the plants were located in four riparian sites and half in five slope sites. Sites were separated by at least 3.2 km to minimize the chance of seed movement between sites. Total fruit crop size and average seed size were estimated for all plants in early August of both years when fruits had just become ripe but had not been removed by frugivores. Fruits were either counted completely (when the total number of fruits was less than 200), in increments of 10 (for fruit crops of 200-1000 fruits), or in increments of 50 (for fruit crops greater than 1000 fruits). Incremental counts were calibrated with complete counts periodically to ensure that they remained accurate. All counts were performed three times and averaged to obtain total fruit crop size. Approximately 15 ripe fruits were sampled randomly from the middle of racemes located in the middle (from top to bottom) of each plant canopy. Digital calipers were used to measure dimensions (width, length and depth) of all collected seeds (i.e., endocarps), and seed volume was calculated with the formula for an ellipsoid (volume =  $(1/6) \cdot \pi \cdot l \cdot w \cdot d$ ). Canopy height, width and depth of all sampled plants were estimated to the nearest 0.5 m.

Before the start of the 1997 and 1998 dispersal seasons (i.e., early August), seed traps (52.1 × 25.4 × 5.7 cm black plastic trays with 1.3 cm mesh hardware cloth covers that excluded predators) were fastened to the ground under plant canopies. Two to six traps ( $\bar{x} = 3$ ; traps covered an average of 2% of total canopy area) were placed under each canopy in 1997, and 3 to

36 traps ( $\bar{x} = 10$ ; traps covered an average of 7% of total canopy area) were placed under each canopy in 1998. Traps remained in place either until all fruits were gone or until remaining fruits were shriveled and unlikely to be removed by frugivores (i.e., by mid October). All *P. virginiana* fruits and seeds that fell into traps were collected from traps weekly.

The formulas listed below were used to calculate (1) number of processed seeds per plant (i.e., all intact seeds with fruit pulp removed by frugivores), (2) number of seeds consumed per plant by legitimate seed dispersers (i.e., seeds from processed fruits that were ingested by frugivores) and (3) number of seeds consumed from plants by seed predators. These variables in turn were used to calculate proportions of processed, consumed or predated seeds per plant (by dividing each by the number of fruits produced per plant).

$$(1) \text{ Number Processed} = N - [(F + P) / a] - R$$

$$(2) \text{ Number Consumed} = N - [(F + D + P) / a] - R$$

$$(3) \text{ Number Predated} = P / a$$

$N$  = Number of fruits produced per plant

$F$  = Naturally-fallen fruits collected in traps (including fruits dropped by frugivores because of small sample sizes)

$P$  = Predated seeds collected in traps (i.e., seeds stripped of pulp, removed from plants and destroyed by avian or mammalian seed predators). This number was estimated by counting the number of predated seeds (i.e., number of seed halves

divided by two) and fruit skins and using the greater of these two numbers.

R = Fruits collected from plants or remaining on plants when seed traps were removed

a = Proportion of canopy area sampled

D = Depulped seeds collected in traps (i.e., non-ingested seeds with pulp removed by frugivores); data available for 1998 only

Because amounts of depulped and consumed seeds were not determined for 1997, comparisons between years were made only for processed seeds. In 1998, all processed seeds collected from traps additionally were classified as either viable or nonviable (i.e., seeds that floated immediately after collection). Because results did not differ when all seeds versus only viable seeds were analyzed, seeds were not separated in analyses presented below. In both years, frugivore preferences for seed size were estimated by comparing the average size of seeds processed by frugivores to the size of seeds in ripe fruits on plants at the beginning of the dispersal season.

#### *Seed Dispersal Patterns:*

Patterns of *P. virginiana* seed dispersal were measured in 1996, 1997 and 1999 by collecting seeds in a combination of seed traps (described above) and 0.26 m<sup>2</sup> quadrats. In 1996, 80 seed traps were placed in a large (i.e., 90 m-wide) riparian corridor that attracted high densities of frugivores (Parson, pers. obs.). The traps were placed 2 m apart in a 14 × 18 m grid centered under 2 fruit-bearing *P. virginiana* in the middle of the corridor. To obtain minimum distances seeds traveled from adult plants, distance of each trap from the nearest fruit-bearing *P. virginiana* was measured (site 1, Table 1; traps within 6.4m of canopies were subsequently assigned to



distance categories equivalent to the prescribed distances used in other sites (below) to obtain averages among sites and years). In 1996, a total of 404 traps also were located in a small (i.e., 15 m-wide) and a medium-sized (i.e., 41-m wide) riparian corridor (sites 2 and 3, Table 1) and in two slope sites (Table 2). To measure seedfall patterns both near and far from *P. virginiana* canopies, traps in these four sites were placed at five geometrically-increasing distances from canopies (Tables 1 and 2). Because of the reduced chance of catching seeds in traps at increased distances from parent plants (Hoppes 1988), trap numbers were increased exponentially with distance (adjacent traps were spaced 1 m apart).

In riparian sites 2 and 3, traps were placed both along and away from the riparian corridor. However, low estimates of seedfall away from corridors (riparian sites) and away from *P. virginiana* canopies (slope sites) may have been conservative. In these relatively open areas, frugivores foraging on the ground appeared to actively avoid seed traps (Parson, pers. obs.). Thus, patterns of seed deposition in these areas were estimated in 1997 by collecting all *P. virginiana* seeds found within quadrats near the end of the dispersal season (i.e., mid to late September, depending on site). In riparian site 1, 90 quadrats were placed at seven geometrically-increasing distances from *P. virginiana* canopies into adjacent upland (Table 1). In addition, *P. virginiana* seeds were collected in a total of 186 quadrats placed in the same pattern around *P. virginiana* canopies in the two slope sites (Table 2). Because seeds on the ground may have been predated before quadrat placement, seed densities ( $d_c$ ) were corrected for predation as follows:

$$d_c = d / (1 - p)^n$$

$d_c$  = corrected seed density

$d$  = uncorrected seed density calculated by counting seeds in  
quadrats

$p$  = site-specific estimate of the proportion of deposited seeds removed per day (see Ch. 3 for methods;  $p = 0.08, 0.17$  and  $0.10$  for site 1 away from the corridor and the two slope sites, respectively; predation rates were averaged within sites since predation did not differ with distance)

$n$  = number of days during which predation was estimated to be substantial;  $n = 7$  was used for all data since seed removal rates for *Prunus* sp. declined substantially after 7 days (Parson, unpubl. data; Whelan et al. 1991; Kollman et al. 1998).\*

\* Because the number of days since seeds were deposited on the ground is unknown,  $n$  (and thus  $d_c$ ) is only an approximation, and absolute values of  $d_c$  were treated with caution. However, this method allowed comparison of the relative shape of seed shadows in open and densely vegetated areas.

To estimate seedfall within riparian corridors in 1997, 90 seeds traps were placed in site 1 and 122 traps in site 4 (i.e., a new site with a 20-m wide corridor; sites 2 and 3 were not used because high 1996 levels of pre-dispersal seed predation resulted in little seedfall into any traps). Traps were placed at seven geometrically-increasing distances from *P. virginiana* canopies, with slightly greater numbers of traps at far distances (Table 1). In 1999, 90 traps each were placed in the corridor of riparian site 1 and in slope site 1 at the distances used in 1997 (Table 1; 90 quadrats also placed at these distances in the slope site provided estimates of dispersal similar to estimates obtained from seed traps; Parson, unpubl. data). To determine the effect of established

perch trees on seed dispersal patterns in 1997, a total of 90 seed traps were placed around two *P. trichocarpa* perch trees within the corridors in each riparian site. Traps were placed at each of five geometrically-increasing distances from the canopy edges of the perch trees in site 1 (i.e., 12 traps each at 0, 0.5, 1.2, and 2.7m and 14 traps at 6.4m; all traps were located at least 6.4m from *P. virginiana* canopies), and at three distances from canopy edges in site 4 (i.e., 10 traps at 0m and 11 traps each at 6.4 and 15m; all traps were located at least 15m from *P. virginiana* canopies). In addition, seven traps were placed under two *P. trichocarpa* canopies and 12 traps under four *P. virginiana* canopies in a riparian site (i.e., site 5) with a 90-m wide corridor and relatively high levels of frugivore activity.

In all years and sites, seed traps were in place for the duration of the dispersal season from mid-August to early October. Fruits and seeds were removed weekly from seed traps and once from quadrats, and classified as fallen fruits, dropped fruits, depulped seeds or consumed seeds (see above for definitions). Dimensions of depulped and consumed seeds were measured with digital calipers (see above). Densities of processed and naturally-fallen seeds were calculated for each distance at which traps or quadrats were placed within sites (i.e., density = number of seeds / (number of traps or quadrats \* trap or quadrat area)). The number and proportion of seeds deposited between distance intervals were calculated for each site by multiplying seed densities for each distance category by the area for which that density was calculated (i.e., area for 0m = average area of *P. virginiana* canopies around which seeds were placed per site; area at 0.5m = area of the concentric ring surrounding the canopy from the canopy edge to 0.5m away, etc.). For distance intervals greater than 0.5m from canopies, the number of deposited seeds was estimated by averaging the seed densities at the inner and outer limits of each concentric ring, and multiplying these average densities by the appropriate ring area. However, the distance interval of 15 - 30m from canopies was not included in the analysis of proportional seed deposition, since

seedfall in this region is increasingly likely to overlap with seedfall from other plants. Both the density and proportion of seeds deposited as a function of distance were averaged among years because patterns were similar among years (Wilcoxon Signed Ranks test;  $Z = -1.05$ ;  $N = 29$ ;  $P = 0.29$ ). Seed densities and proportions were subsequently averaged among all sites tested in each habitat because patterns appeared to be similar among sites (however, small sample sizes prevented statistical comparison between sites).

To obtain additional information on the foraging and post-foraging behavior of avian frugivores, frugivores were observed in riparian site 5 in 1997 (low densities or infrequent occurrences of frugivores in other sites made collection of sufficient data impossible). Observations were made daily throughout the dispersal season during the period of peak foraging activity (i.e., 0645 to 0945). For frugivores that foraged in flocks (i.e., *B. cedrorum*), only one individual was observed per flock to ensure that data were independent. For each frugivore observed, variables recorded included frugivore species, distance and direction of post-foraging flights (measured as degrees and categorized as eight cardinal directions for analysis), and species of post-foraging perch locations.

#### *Data Analysis:*

To obtain normally-distributed variables for statistical analysis, fruit crop size, seed size, canopy volume, number of processed, consumed and predated seeds, duration of foraging and number of fruits eaten per visit were  $\log_{10}$ -transformed, and proportions of processed and consumed seeds were arcsine-square root transformed. However, the transformed proportions of processed and consumed seeds were only normally-distributed when plants that were not "visited" by frugivores or legitimate seed dispersers (i.e., plants with values of zero for these variables; Murray 1987) were removed from analysis. In addition, the proportion of predated seeds removed from plants

visited by seed predators could not be transformed to a normal distribution. Thus, tests that included all plants and tests of proportional seed predation for visited plants were nonparametric, while tests of visited plants for all other dependent variables were parametric.

Kruskal-Wallis tests were used to compare the number or proportion of seeds processed, consumed or predated from all plants between habitats and years ( $\alpha = 0.05$ ; to provide Bonferroni corrections for multiple tests, p-values for tests of processed and consumed seeds were multiplied by 6, and p-values for tests of predated seeds were multiplied by 4). Spearman's Correlations were used to test associations between these variables and fruit crop size or seed size (effects of canopy size also were tested because of its potential effect on frugivore or predator preferences;  $\alpha = 0.05$ ; to provide Bonferroni corrections, p-values for tests of processed and consumed seeds were multiplied by 12, and p-values for tests of predated seeds were multiplied by 6). Logistic Regressions were used to test the association between habitat, year, crop size, seed size and canopy size (two-way interactions were only included in final models if significant) and the likelihood that plants were visited by frugivores, seed dispersers or predators ( $\alpha = 0.05$ ; p-values for tests of visitation by frugivores or seed dispersers were multiplied by 2 to provide a Bonferroni correction).

For visited plants, Multiple Regression was used to test the association between habitat, year, fruit crop size, average seed size and canopy size and the number or proportion of seeds processed, consumed or predated. Because of small sample sizes, tests of visited plants were conducted at  $\alpha = 0.1$  (to provide Bonferroni corrections, p-values for tests of processed and consumed seeds were multiplied by 4, and p-value for the test of number of predated seeds was multiplied by 2, although proportion of predated seeds was analyzed in nonparametric tests). For the proportion of predated seeds, Kruskal-Wallis tests were used to analyze habitat and year

effects (p-values were multiplied by 2 to provide a Bonferroni correction), and Spearman's Correlations were used to test associations between the proportion of predated seeds and fruit crop size, seed size and canopy size (p-values were multiplied by 3 to provide a Bonferroni correction).

In the tests described above, the proportions of processed, consumed and predated seeds did not vary with habitat, crop size or seed size. Thus, statistical results for these tests are not reported. In addition, results for amounts of processed and consumed seeds did not differ, and only results for amounts of processed seeds are reported.

Paired t-tests were used to compare the average volume of seeds on plants to the average volume of processed, depulped (1998 only) or consumed (1998 only) seeds under plants in each habitat ( $\alpha = 0.05$ ; to provide Bonferroni corrections, p-values were multiplied by 2 for 1997 data and by 6 for 1998 data). Because these tests assumed that seeds deposited by frugivores under plants originated from those plants, additional paired t-tests were conducted to compare seed size differences for entire sites (i.e., seed size on plants averaged per site versus processed, depulped or consumed seed sizes per site). However, results for within-site comparisons did not differ from within-plant comparisons, and only the latter are presented below. To determine whether single dimensions of seed size were driving the relationship between consumed and nonconsumed seeds, the sizes of produced and processed seeds also were compared in terms of seed width, length and depth (1997 and 1998; both habitats combined;  $\alpha = 0.05$ ; p-values were multiplied by 6 to provide a Bonferroni correction).

Seed densities could not be transformed to normal distributions; thus, Spearman's Correlations ( $\alpha = 0.1$  because of small sample sizes) were used to test correlations between processed or naturally-fallen seed density and distance from *P. virginiana* canopies (p-values were multiplied

by 6 to provide a Bonferroni correction because two tests each were conducted for riparian habitat within corridors, riparian habitat away from corridors and slope habitat). Spearman's Correlations were used to test correlations between processed seed density and distance from *P. trichocarpa* canopies ( $\alpha = 0.1$ ; riparian habitat only). Chi-square tests ( $\alpha = 0.1$ ) were used to determine whether frugivores chose nonrandom arrival and departure directions (of eight cardinal directions). Chi-square tests ( $\alpha = 0.1$ ) also were used to determine whether frugivores chose nonrandom post-foraging perch sites within the three most common potential perch species (i.e., *P. virginiana*, *P. trichocarpa* and *P. tremuloides*; expected frequencies for use as perch sites were calculated based on the number of individuals of each species within the site). Spearman's Correlations were used to test the association between frugivores (i.e., number) and the distance traveled to post-foraging perch sites ( $\alpha = 0.1$ ; riparian habitat only; preliminary data from 1996 combined with 1997 data to increase sample size).

## RESULTS

### *Fruit Consumption and Seed Predation / Among-Plant Preferences:*

The likelihood of plant visitation by frugivores, seed dispersers or seed predators was not influenced by habitat or canopy size, but visitation by frugivores was greater in 1998 than in 1997 (Tables 3 and 4). Fruit crop size and seed size influenced chances of visitation by seed predators but not by frugivores or seed dispersers (Table 4). However, effects of these traits on the likelihood of seed predation varied with habitat (Table 4). Plants with large crop sizes experienced slightly increased visitation by seed predators on slopes but not in riparian habitat (however, within-habitat effects were not significant in posthoc tests). Plants in riparian habitat tended to have relatively large numbers of processed seeds and predated seeds (Table 5). However, the only trend that approached significance was the difference in number of predated

seeds between habitats (Table 6). In both habitats, more seeds were processed in 1998 than in 1997, but similar amounts of seeds were predated in both years (Tables 5 and 6). Fruit crop size was not associated with number of processed seeds, but was positively associated with number of predated seeds (Table 7; however, this association was only apparent in slope habitat; Fig. 1).

For plants visited by frugivores (i.e., plants with at least one seed processed by frugivores), the number of processed seeds varied between years but was strongly positively associated with fruit crop size in both years (Table 9a; Fig. 2). For plants visited by seed predators, the number of predated seeds did not vary with year, habitat, crop size, seed size or canopy size (Table 9b).

#### *Fruit Consumption / Within-Plant Preferences:*

In slope habitat, seeds produced by plants were larger than processed and consumed seeds, but did not differ in size from depulped seeds (Fig. 3). In riparian habitat, seeds produced by plants did not differ in size from processed, depulped or consumed seeds (Fig. 3). When seed dimensions were analyzed rather than seed volume (both habitats combined; 1998 only), seeds produced by plants were larger in width and depth (1998 only) than processed seeds, but did not differ in length (Fig. 4).

#### *Seed Dispersal Patterns:*

Densities of naturally-fallen and processed seeds declined rapidly beyond plant canopies and were significantly negatively correlated with distance in both riparian and slope habitat (Fig. 5a). However, processed seed densities in riparian habitat were negatively correlated with distance only away from corridors (Fig. 5b). Overall, a substantial proportion of processed seeds (i.e., 62.0%) was likely to be moved away from adult *P. virginiana* canopies in riparian habitat, while



less than half the processed seeds (i.e., 29.0%) were moved away from adult canopies in slope habitat (Fig. 6).

Densities of processed seeds under *P. trichocarpa* perch trees in riparian sites 1 and 4 were low relative to densities under *P. virginiana* canopies and declined only slightly with distance (Fig. 5c). In contrast to these sites, the density of processed *P. virginiana* seeds under *P. trichocarpa* canopies in riparian site 5 was extremely high (i.e., 671 seeds / m<sup>2</sup>), and was approximately 3 times greater than the density of processed seeds under *P. virginiana* canopies (i.e., 211 seeds / m<sup>2</sup>).

Avian frugivores in riparian site 5 (primarily *B. cedrorum*) departed from plants along the riparian corridor (data available for 1997 only; Fig. 7;  $X^2 = 58.38$ ;  $N = 106$ ;  $P \leq 0.0005$ ). After foraging, most birds (98%; total  $N = 103$ ) perched in trees or shrubs in the site rather than flying off site. Frugivores discriminated among the three most common post-foraging perch locations in site 5, perching more than expected in *P. trichocarpa* and less than expected in *P. virginiana* and *P. tremuloides* ( $X^2 = 114.95$ ;  $N = 131$ ;  $P < 0.0005$ ; data from 1996 and 1997 combined). Half of the birds that perched after foraging moved at least 15 m, and 22% traveled at least 30 m before perching. As a result, frugivore numbers did not decline with distance between foraging and perch sites ( $\rho = -0.27$ ;  $N = 17$ ;  $P = 0.30$ ).

## DISCUSSION

### *Fruit Consumption and Seed Predation / Among-Plant Preferences:*

This study indicates that large seed number may play an important role in the dispersal success of a fleshy-fruited plant, as a result of its influence on the selection of fruits by frugivores.

Frugivores removed greater numbers but not proportions of *P. virginiana* fruits from plants with large fruit crops, which is consistent with research on other fleshy-fruited plants (Alcantara et al. 1997; Howe and De Steven 1979; Murray 1987; Sallabanks 1992; Jordano 1995). The preference of frugivores for large crop sizes also is consistent with previous research on *B. cedrorum* and *T. migratorius*, the two primary frugivore species that forage on *P. virginiana* (McPherson 1987; Sallabanks 1993). The large fruit crops of riparian plants thus may be produced to enhance seed processing or consumption by frugivores. However, numbers of fruits processed by frugivores did not differ significantly between habitats, most likely because of substantial within-habitat variation in fruit removal (Table 5 and 8a). In addition, frugivore preference for large crop size was apparent in slope as well as riparian habitat (Table 9a). The consistent production of small crop sizes on slopes indicates that resource limitation or selection pressures other than those imposed by frugivores may be more predominant in this environment.

The likelihood of visitation by frugivores did not vary with habitat or fruit crop size, suggesting that frugivores used other cues to choose among plants. Frugivore visitation may be influenced by extrinsic factors such as removal of seeds by vertebrate predators. *P. virginiana* plants that received high levels of vertebrate seed predation, for example, were not as likely to be visited by frugivores (Chi-square tests of the association between likelihood of frugivore visitation and the number and proportion of predated seeds:  $X^2 = 11.18$  and  $11.45$ , respectively;  $N = 67$ ;  $P = 0.001$ ). In contrast, plants visited by frugivores had large amounts of seeds processed by frugivores (Table 8a) relative to amounts destroyed by seed predators in both years (e.g.,  $\bar{x} \pm 1$  SD =  $58 \pm 128$  seeds predated per riparian plant and  $22 \pm 64$  per slope plant). Relatively high levels of seed predation in riparian habitat (Tables 3,5 and 6) may have limited the number of plants suitable for foraging and masked frugivore preferences for plant traits.

Seed predation was slightly higher in riparian habitat than on slopes, but riparian plants with large crops did not experience lower seed predation than plants with small crops. In slope habitat, fruit crop size in fact was associated with slightly *increased* predation (Tables 4 and 7; Fig. 1), although proportional predation did not vary. Thus, large *P. virginiana* fruit crops do not appear to satiate vertebrate seed predators, even in the habitat where predation may be more predominant.

*Fruit Consumption / Within-Plant Preferences:*

Frugivores did not discriminate among maternal *P. virginiana* plants based on seed size, but chose smaller seed dimensions within plants (Figs. 3 and 4). This pattern is consistent with the hierarchical selection regime previously documented for avian frugivores, in which shrubs are selected based on fruit crop size, but fruits are selected within shrubs based on fruit or seed size (Sallabanks 1992, 1993; Jordano 1995). Because seed number and size are often negatively correlated, selection on plant traits at different levels is not necessarily discordant. Large maternal crop sizes and small individual seed sizes are components of one of two reproductive strategies that are likely to evolve in resource-limited environments (Ch. 1 and references therein). Thus, frugivore preferences for these traits may result in relatively strong net selection for the production of many small seeds in environments where seed dispersal is important.

The preference of legitimate seed dispersers for small seeds in slope habitat, where plants produce relatively large seeds, is consistent with the preference of *B. cedrorum* for small fruits and seeds (McPherson 1987). Although the net effect of frugivore preferences for seed size may vary depending on the proportion of each legitimate frugivore species present (*T. migratorius*, for example, has been found to prefer large fruits over small ones; Murray 1993; Sallabanks 1993), *B. cedrorum* forages in large flocks and appears to be the dominant consumer of *P. virginiana*

seeds in both slope and riparian habitat in western Montana (Parson, pers. obs.). The small size of consumed seeds but not depulped seeds relative to produced seeds suggests that frugivores consume small fruits as a result of gape width limitations or increased handling efficiency, but are less restricted by seed size when seeds are not ingested (Levey 1987; Rey et al. 1997). In addition, frugivore species that depulp seeds may differ from those that consume seeds. House finches (*Carpodacus mexicanus*), for example, were observed depulping but never ingesting seeds in both habitats. The significant differences in seed width and depth between produced and consumed seeds indicate that frugivores may select fruits based on one or a combination of these dimensions rather than length. Birds typically swallow fruits lengthwise (Parson, pers. obs.; Wheelwright 1985), and seed width and depth are the two dimensions most likely to determine whether a seed can be ingested. Because avian seed consumers are the most likely dispersers of *P. virginiana* seeds, their preference for small seed size may impose selection pressure on *P. virginiana* reproductive strategies. The production of large seeds in slope habitat despite this preference indicates that seed dispersal is outweighed by selection pressures favoring large seed size in this environment. Frugivores did not exhibit within-plant seed size preferences in riparian habitat, but all seeds were relatively small in this environment.

#### *Seed Dispersal Patterns:*

In riparian habitat, primary dispersal by avian frugivores extended the tail of the seed shadow a substantial distance beyond *P. virginiana* canopies where seeds naturally fall (Figs. 5a and 6). In contrast, *P. virginiana* seeds processed by frugivores in slope habitat were not moved farther than naturally-fallen seeds, and were deposited primarily under adult canopies. This variation in seed shadows was associated with clear differences in seed and fruit crop size between habitats, and suggests that the reproductive strategy of riparian plants enhances dispersal. Plants in riparian habitat possessed large fruit crops, which were associated with relatively large numbers of seeds

consumed by frugivores. As a result these plants were likely to have large numbers of seeds dispersed away from parent canopies. Plants in slope habitat, in contrast, possessed small crops of large seeds that were associated with decreased chances of consumption and thus potential seed dispersal by frugivores. Although many studies have examined the importance of plant traits for seed dispersal, the seed shadows created by frugivores have rarely been linked to environmental variation in plant traits (but see Herrera 1981).

Differences in the structural components of habitats also may contribute to variation in patterns of seed deposition (e.g., McDonnell and Stiles 1983; reviewed in Schupp and Fuentes 1995). In riparian habitat, frugivores oriented their post-foraging flights in a linear directional pattern along corridors (Fig. 7), and consequently moved seeds farther distances along versus away from corridors (Fig. 5c). The continuous presence of potential perch sites along corridors and lack of perch sites away from corridors may explain the difference in frugivore movement and seed deposition between these areas. Vegetation used as post-foraging perch sites often is associated with secondary peaks in seed shadows (e.g., Fuentes et al. 1986; Hoppes 1988; Chavez-Ramirez and Slack 1994; Toh et al. 1999). The role of individual perch trees as focal points for seed deposition was particularly evident in riparian site 5, where *P. trichocarpa* and other large trees occurred in low densities relative to riparian sites 1 and 4 (Parson, pers. obs.). In slope habitat, the scarcity of perch sites other than *P. virginiana* may largely explain the short distances seeds traveled from adult conspecifics (Parson, pers. obs.). However, the extent to which perch sites influence *P. virginiana* seed shadows cannot be separated from effects of plant traits on seed shadows (above) because these hypotheses are not mutually exclusive.

Seed movement between habitats will decrease intergenerational environmental correlations and thus decrease the chance that plants develop specialized reproductive strategies in each habitat (Van Tienderen 1991). Although the degree to which seeds were moved between habitats was

not estimated, movement between habitats was probably minimal relative to movement within habitats for two reasons: most *P. virginiana* on slopes in western Montana are not immediately adjacent to *P. virginiana* in riparian corridors (Parson, pers. obs.), and patterns of seed deposition within habitats (i.e., along corridors in riparian habitat and under *P. virginiana* canopies in slope habitat) indicate that seeds are likely to remain in those habitats. Consistent maternal reproductive strategies within each habitat thus may increase the chance of seed deposition in predictable locations, which in turn may increase chances of successful seedling establishment (see Ch. 3 for further development of this hypothesis).

## SUMMARY

The strength of selection pressures imposed on *P. virginiana* by frugivores is likely to be influenced by the spatial and temporal consistency of frugivore foraging patterns (e.g., Herrera 1985). *P. virginiana* seed shadows varied substantially between habitats, but were similar within habitats and among years. Further experimental approaches are necessary to determine the relative importance of *P. virginiana* reproductive traits to patterns of seed deposition, and thus to determine which reproductive phenotype is the most adaptive for seed dispersal. However, the evidence presented here strongly suggests that production of large numbers of *P. virginiana* seeds increases chances of dispersal (from the perspective of the maternal plant), while production of large seeds decreases chances of dispersal (of individual seeds). Ultimately, seed number and size may interact with the location in which they fall to influence offspring survival and establishment. Further research thus is critical to measure the effects of these dispersal patterns on the successive stages in the recruitment process, and to determine whether dispersal itself is adaptive (i.e., directed to locations where offspring recruitment is most likely).

## LITERATURE CITED

- Alcantara, J. M., P. J. Rey, F. Valera, A. M. Sanchez-Lafuente and J. E. Gutierrez. 1997. Habitat alteration and plant intra-specific competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. *Oikos* 79: 291-300.
- Augsburger, C. K., and K. Kitajima. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73: 1270-1284.
- Baker, K. B., A. J. Richards, and M. Tremayne. 1994. Fitness constraints on flower number, seed number and seed size in the dimorphic species *Primula farinosa* L. and *Armeria maritima* (Miller) Willd. *New Phytol.* 128: 563-570.
- Bronstein, J. L. and K. Hoffmann. 1987. Spatial and temporal variation in frugivory at a Neotropical fig, *Ficus pertusa*. *Oikos* 49: 261-268.
- Chavez-Ramirez, F., and R. D. Slack. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. *Oikos* 71: 40-46
- Crawley, M. J. 1992. Seed predators and plant population dynamics. *In*: Fenner, M. (ed.). The ecology of regeneration in plant communities. CAB International, Wallingford, Oxon. pp. 157-192.
- Denslow, J.S. and T. C. Moermond. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: An experimental study. *Oecologia* 54: 170-176.
- Donohue, K. 1998. Maternal determinants of seed dispersal in *Cakile edentula*: fruit, plant, and site traits. *Ecol.* 79: 2771-2788.
- Donohue, K. 1999. Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *Am. Nat.* 154: 674-689.

- Donohue, K. and J. Schmitt. 1998. Maternal environmental effects in plants: Adaptive plasticity? *In: Mousseau, T. A. and C. W. Fox (eds.). Maternal effects as adaptations.* Oxford Univ. Press, New York.
- Foster, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Bot. Rev.* 52: 260-299.
- Fuentes, E. R., A. J. Hoffman, A. Poiani, and M. C. Alliende. 1986. Vegetation change in large clearings: patterns in the Chilean matorral. *Oecologia* 68: 358-366.
- Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monogr.* 61: 183-206.
- Gross, K. L and A. D. Smith. 1991. Seed mass and emergence time effects on performance of *Panicum dichotomiflorum* Michx. across environments. *Oecologia* 87: 270-278.
- Guitan, J., M. Fuentes, T. Bermejo, and B. Lopez. 1992. Spatial variation in the interactions between *Prunus mahaleb* and frugivorous birds. *Oikos* 63: 125-130.
- Herrera, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36: 51-58.
- Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44: 132-141.
- Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr.* 68: 511-538.
- Herrera, C. M., P. Jordano, L. Lopez-Soria and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.* 64: 315-344.
- Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* 69: 320-329.



- Horvitz, C. C. and D. W. Schemske. 1986. Seed dispersal and environmental heterogeneity in a neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica*: 18: 319-323.
- Horvitz, C. C. and D. W. Schemske. 1990. Spatiotemporal variation in insect mutualists of a neotropical herb. *Ecology* 71: 1085-1097.
- Horvitz, C. C. and D. W. Schemske. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* 75: 1949-1958.
- Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecol.* 61: 944-959.
- Howe, H. F. 1990. Survival and growth of juvenile *Virola surinamensis* in Panama: Effects of herbivory and canopy closure. *J. Tropical Ecol.* 6: 259-280.
- Howe, H. F. and De Steven. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* 39: 185-196.
- Howe, H. F. and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111: 817-832.
- Howe, H. F. and W. M. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347-351.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781-791.
- Howe, H. F. and G. A. Vande Kerckhove. 1980. Nutmeg dispersal by tropical birds. *Science* 210: 925-927.
- Howe, H. F. and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093-1106.
- Hulme, P. E. 1994. Post-dispersal seed predation in grassland: Its magnitude and sources of variation. *J. Ecol.* 82: 645-652.
- Janzen, D. H. 1976. Why bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* 7: 347-391.

- Jordano, P. 1993. Geographical ecology and variation of plant-disperser interactions: southern Spanish junipers and frugivorous thrushes. *Vegetatio* 107/108: 85-104.
- Jordano, P. 1995. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* 76: 2627-2639.
- Kollman, J., D. A. Coomes and S. M. White. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Funct. Ecol.* 12: 683-690.
- Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129: 471-485.
- Lott, R. H., G. N. Harrington, A. K. Irvine and S. McIntyre. 1995. Density-dependent seed predation and plant dispersion of the tropical palm *Normanbya normanbyi*. *Biotropica* 27: 87-95.
- Malmborg, P. K. and M. F. Willson. 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois (USA) woodlot. *Condor* 90: 173-186.
- Marshall, D. L. 1986. Effect of seed size on seedlings success in three species of *Sesbania* (Fabaceae). *Am. J. Bot.* 73: 457-464.
- Martin, T. E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* 66: 563-573.
- Mazer, S. J. and L. M. Wolfe. 1998. Density-mediated maternal effects on seed size in wild radish: Genetic variation and its evolutionary implications. In: Mousseau, T. A. and C. W. Fox (eds.). *Maternal effects as adaptations*. Oxford Univ. Press, New York.
- McDonnell, M. J. and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109-116.
- McGinley, M. A. 1989. Within and among plant variation in seed mass and pappus size in *Tragopogon dubius*. *Can. J. Bot.* 67: 1298-1304.

- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159-191 in L. E. Gilbert and P. H. Raven (eds.). *Coevolution of animals and plants*. Univ. of Texas Press, Austin.
- McPherson, J. M. 1987. A field study of winter fruit preferences of cedar waxwings. *Condor* 89: 293-306.
- McPherson, J. M. 1988. Preferences of cedar waxwings in the laboratory for fruit species, color and size: a comparison with field observations. *Anim. Behav.* 36: 961-969.
- Meyer, G. A. and M. C. Witmer. 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *Am. Midl. Nat.* 140: 129-139.
- Morse, D. H. and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. *Oecologia* 67: 372-379.
- Murray, K. G. 1987. Selection for optimal fruit crop size in bird-dispersed plants. *Am. Nat.* 129: 18-31.
- Murray, K. G. 1993. The influence of seed packaging and fruit color on feeding preferences of American Robins. *Vegetatio* 107/108: 217-226.
- Myster, R. W. and S. T. A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree and seed predation in old fields. *Oikos* 66: 381-388.
- Notman, E., D. L. Gorchov and F. Cornejo. 1996. Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species. *Oecologia* 106: 221-227.
- Piper, J. K. 1986. Effects of habitat and size of fruit display on removal of *Smilacina stellata* (Liliaceae) fruits. *Can. J. Bot.* 64: 1050-1054.
- Platt, W. J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). *Oecologia* 22: 399-409.

- Platt, W. J., and I. M. Weis. 1985. An experimental study of competition among fugitive prairie plants. *Ecology* 66:708-720.
- Pratt, T. K. and E. W. Stiles. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *Am. Nat.* 122: 797-805.
- Rey, P. J., E. Guitierrez, J. Alcantara and F. Valera. 1997. Fruit size in wild olives: implications for avian seed dispersal. *Funct. Ecol.* 11: 611-618.
- Russell, S. K. and E. W. Schupp. 1998. Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). *Oikos* 81: 434-443.
- Sallabanks, R. S. 1992. Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn. *Crataegus monogyna* (Rosaceae). *Oecologia* 91: 296-304.
- Sallabanks, R. S. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326-1336.
- Schupp, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76: 525-530.
- Schupp, E. W. 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51: 71-78.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82: 399-409.
- Schupp, E. W. and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2: 267-275.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* 14: 235-250.
- Sultan, S. E. and F. A. Bazzazz. 1993. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution* 47: 1009-1031.

- Toh, I., M. Gillespie and D. Lamb. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecol.* 7: 288-297.
- Van Tienderen, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution*: 45: 1317-1331.
- Webb, S. L., and M. F. Willson. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67: 150-153.
- Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808-818.
- Wheelwright, N. T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Vegetatio* 107/108: 163-174.
- Whelan, C. J., M. F. Willson, C. A. Tuma and I. Souza-Pinto. 1991. Spatial and temporal patterns of post-dispersal seed predation. *Can. J. Bot.* 69: 428-36.
- Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*: 107/108: 261-280.
- Willson, M. F. and F. H. J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. *J. Tropical Ecol.* 5: 301-308.
- Willson, M. F., and C. J. Whelan. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: Effects of density, habitat, location, season, and species. *Oikos* 57: 191-198.
- Willson, M. F., and C. J. Whelan. 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. *Ecol. Monogr.* 63: 151-172.
- Winn, A. A. 1988. Ecological and evolutionary consequences of seed size in *Prunella vulgaris*. *Ecology* 69: 1537-1544.
- Wulff, R. D. 1986. Seed size variation in *Desmodium Paniculatum*: I. Factors affecting seed size. *J. Ecol.* 74: 87-97.

**Table 1.** Total number of seed traps or quadrats placed at seven distances from fruit-bearing *P. virginiana* canopies in riparian habitat, 1996, 1997 and 1999.

Distance (m)	Orientation relative to riparian corridor					
	1996		1997		1999	
	Along (Site 1) <sup>a</sup>	Along (Sites 2 + 3)	Away (Sites 2 + 3)	Along (Sites 1 + 4)	Away (Site 1) <sup>b</sup>	Along (Site 1)
0	24	---	---	24	5	12
0.5	4	2	2	25	5	12
1.2	7	2	2	24	5	12
2.7	13	4	4	24	5	12
6.4	27	12	12	37	10	14
8.5	5	---	---	---	---	---
15	---	60	60	39	20	14
30	---	---	---	39	40	14

**a** Traps assigned to each distance category include all traps at that distance or at distances greater than the previous category

**b** Quadrats were used at all distances

**Table 2.** Total number of seed traps or quadrats placed at 7 distances from fruit-bearing *P. virginiana* canopies in two sites in slope habitat, 1996, 1997 and 1999.

Distance (m)	1996	1997 <sup>a</sup>	1999
0	---	12	12
0.5	6	12	12
1.2	6	12	12
2.7	12	12	12
6.4	36	20	14
15	180	36	14
30	---	82	14

<sup>a</sup> Quadrats were used at all distances

**Table 3.** Likelihood of visitation to *P. virginiana* plants by frugivores, legitimate seed dispersers or seed predators in riparian and slope habitat, 1997-1998.

Type of visitation	Year			
	1997		1998	
	Riparian (N = 17)	Slope (N = 15)	Riparian (N = 17)	Slope (N = 16)
Plants visited by frugivores <sup>a</sup> (%)	18	20	65	81
Plants visited by seed dispersers <sup>b</sup> (%)	---	---	47	75
Plants visited by seed predators <sup>c</sup> (%)	65	33	65	38

<sup>a</sup> Plants with one or more seeds processed (i.e., depulped or consumed) by frugivores

<sup>b</sup> Plants with one or more seeds consumed by frugivores

<sup>c</sup> Plants with one or more seeds predated from fruits



**Table 4.** Logistic regression results for the likelihood of visitation to *P. virginiana* plants by frugivores, legitimate seed dispersers or seed predators (vs. year, habitat, crop size, seed size, canopy size and all significant two-way interactions), 1997-1998.

Type of visitation	Overall Model <sup>a</sup>			Model if Terms Removed <sup>b</sup>		
	N	X <sup>2</sup>	P <sup>c</sup>	Covariates	Deviance	P <sup>c</sup>
Frugivores	65	21.83	<b>0.0011</b>	Habitat <b>Year</b> Crop Size Seed Size Canopy Size	0.62 <b>17.88</b> 0.014 0.033 0.81	0.86 <b>&lt;0.0001</b> 1.00 1.00 0.73
Seed dispersers <sup>d</sup>	33	2.86	1.00	---	---	---
Seed predators	65	21.45	<b>0.0060</b>	Habitat Year <b>Crop Size</b> <b>Seed Size</b> Canopy Size <b>Crop*Hab</b> <b>Seed*Hab</b> <b>Crop*Seed</b>	1.75 0.77 10.16 8.80 0.26 12.01 5.62 9.44	0.19 0.38 <b>0.0014</b> <b>0.0030</b> 0.61 <b>0.00053</b> <b>0.018</b> <b>0.0021</b>

<sup>a</sup> Omnibus test results of model coefficients for the first step of the Backward Stepwise (Likelihood Ratio) method

<sup>b</sup> For significant models, the deviance is the change in -2 log likelihood if each covariate is removed individually from the model

<sup>c</sup> Significant tests at  $\alpha = 0.05$  indicated in bold (p-values have been multiplied by 2 for frugivore and seed disperser visitation)

<sup>d</sup> Data available for 1998 only

**Table 5.** Number and proportion of *P. virginiana* seeds processed or predated per plant in riparian and slope habitat, 1997-1998.

Seed Fate	Year			
	1997		1998	
	Mean (SD)		Mean (SD)	
	Riparian (N = 17)	Slope (N = 15)	Riparian (N = 17)	Slope (N = 16)
Processed (#)	323 (1007)	43 (130)	739 (964)	253 (350)
Processed (%)	9 (21)	6 (16)	41 (36)	55 (33)
Predated (#)	1311 (2591)	544 (1365)	1073 (1719)	127 (284)
Predated (%)	40 (47)	27 (43)	38 (48)	15 (34)

**Table 6.** Kruskal-Wallis test results for habitat and year effects on the number of seeds processed or predated per *P. virginiana* plant in riparian and slope habitat, 1997-1998.

Factor	Dependent Variable	$\chi^2$	N	P
Habitat	Processed Seeds <sup>a</sup>	0.090	65	1.00
	Predated Seeds <sup>b</sup>	6.00	65	0.056
Year	<b>Processed Seeds<sup>a</sup></b>	15.96	67	<b>0.0004</b>
	Predated Seeds <sup>b</sup>	0.19	67	1.00

<sup>a</sup> Tests significant at  $\alpha = 0.05$  indicated in bold (p-values have been multiplied by 6)

<sup>b</sup> No tests significant at  $\alpha = 0.05$  (p-values have been multiplied by 4)

**Table 7.** Spearman's Correlations between fruit crop size, seed size or canopy size and the number of seeds processed or predated per *P. virginiana* plant in riparian and slope habitat, 1997-1998.

Factor	Dependent Variable	rho	N	P
Crop Size	Processed Seeds <sup>a</sup>	0.046	67	1.00
	<b>Predated Seeds<sup>b</sup></b>	0.40	67	<b>0.006</b>
Seed Size	Processed Seeds <sup>a</sup>	-0.038	67	1.00
	Predated Seeds <sup>b</sup>	-0.30	67	0.084
Canopy Size	Processed Seeds <sup>a</sup>	0.059	67	1.00
	Predated Seeds <sup>b</sup>	-0.002	67	1.00

<sup>a</sup> No tests significant at  $\alpha = 0.05$  (p-values have been multiplied by 12)

<sup>b</sup> Tests significant at  $\alpha = 0.05$  indicated in bold (p-values have been multiplied by 6)

**Table 8.** Number and proportion of *P. virginiana* seeds (a) processed per plant from plants visited by frugivores, or (b) predated per plant from plants visited by seed predators in riparian and slope habitat, 1997-1998.

Seed Fate & Type of visitation	Metric	Year			
		1997		1998	
		Mean (SD)		Mean (SD)	
(a)	#	Riparian	Slope	Riparian	Slope
		1831 (1992) N = 3	215 (250) N = 3	1142 (990) N = 11	311 (365) N = 13
	%	50 (21) N = 3	30 (25) N = 3	64 (22) N = 11	67 (21) N = 13
(b)	#	2026 (3024) N = 11	1631 (2075) N = 5	1658 (1913) N = 11	337 (396) N = 6
		62 (45) N = 11	82 (28) N = 5	59 (48) N = 11	41 (46) N = 6

**Table 9.** Partial regression coefficients for habitat, year, fruit crop size, seed size and canopy volume effects on the number of *P. virginiana* seeds (**a**) processed per plant from plants visited by frugivores, or (**b**) predated per plant from plants visited by seed predators in riparian and slope habitat, 1997-1998.

Dependent Variable	Independent Variable	$r^2$	P
<b>a<sup>a,b</sup></b>	Habitat	0.21	1.00
	<b>Year</b>	0.50	<b>0.032</b>
	<b>Crop Size</b>	0.89	<b>&lt;0.0001</b>
	Seed Size	-0.18	1.00
	Canopy Size	-0.094	1.00
<b>b<sup>c,d</sup></b>	Habitat	0.054	1.00
	Year	0.14	0.94
	Crop Size	0.29	0.24
	Seed Size	-0.27	0.32
	Canopy Size	-0.24	0.42

<sup>a</sup> Tests significant at  $\alpha = 0.1$  indicated in bold (p-values have been multiplied by 4)

<sup>b</sup>  $R^2 = 0.86$ ;  $F = 31.46$ ;  $df = 5, 25$ ;  $P < 0.0005$

<sup>c</sup> No tests significant at  $\alpha = 0.1$  (p-values have been multiplied by 2)

<sup>d</sup>  $R^2 = 0.32$ ;  $F = 2.60$ ;  $df = 5, 28$ ;  $P = 0.047$

## FIGURE LEGENDS

**Figure 1.** Association between *P. virginiana* fruit crop size and number of seeds predated per plant in riparian and slope habitat, 1997-1998 (Spearman's rho for slope habitat = 0.42; rho for riparian habitat = 0.14). Number of predated seeds is not log-transformed so that results can be seen for all plants (including those with no predated seeds).

**Figure 2.** Partial regression plot of the association between *P. virginiana* fruit crop size and the number of fruits processed per plant by frugivores (effects of year, habitat, seed size and canopy size have been removed).

**Figure 3. (a)** Difference between average seed size ( $\text{mm}^3$ ) per plant and processed seed size per plant for *P. virginiana* plants in riparian and slope habitat, 1997 and 1998 ( $\alpha = 0.05$ ; p-values multiplied by 2). In paired t-tests:  $t = -0.71$ ,  $P = 0.98$  (riparian 1997);  $t = -0.55$ ,  $P = 1.00$  (riparian 1998);  $t = 4.18$ ,  $P = 0.002$  (slope 1997);  $t = 5.67$ ,  $P < 0.0001$  (slope 1998). **(b)** Difference between average seed size per plant and consumed or depulped seed size per plant for *P. virginiana* plants in riparian and slope habitat; 1998 only ( $\alpha = 0.05$ ; p-values multiplied by 6). In paired t-tests:  $t = -2.82$ ,  $P = 0.072$  (riparian; depulped);  $t = 0.74$ ,  $P = 1.00$  (riparian; consumed);  $t = 2.89$ ,  $P = 0.089$  (slope; depulped);  $t = 4.57$ ,  $P = 0.006$  (slope; consumed). Significant differences from zero are indicated by asterisks.

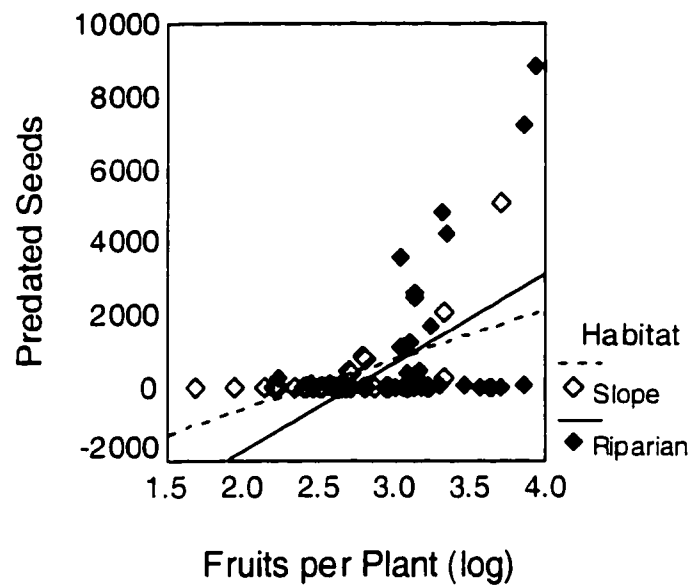
**Figure 4.** Difference between average seed size (mm) per plant and processed seed size per plant for *P. virginiana* plants (riparian and slope habitats combined), 1997 and 1998 ( $\alpha = 0.05$ ; p-values multiplied by 6). In paired t-tests:  $t = 2.79$ ,  $P = 0.053$  (seed width, 1997);  $t = 2.07$ ,  $P = 0.28$  (seed length 1997);  $t = 1.54$ ,  $P = 0.78$  (seed depth 1997);  $t = 3.42$ ,  $P = 0.010$  (width, 1998);  $t = 1.87$ ,  $P = 0.41$  (length, 1998);  $t = 3.29$ ,  $P = 0.014$  (depth, 1998). Significant differences from zero are indicated by asterisks.

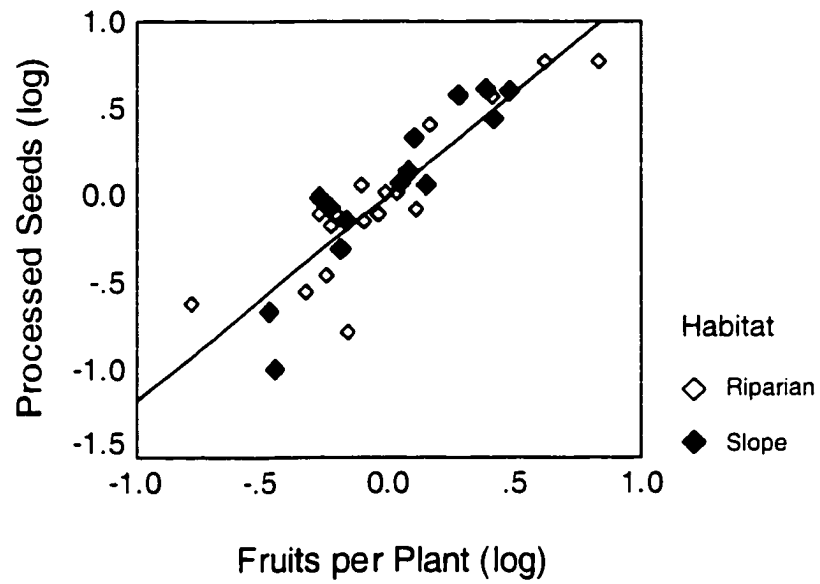
**Figure 5. (a)** Densities of processed ("Proc") and naturally-fallen *P. virginiana* seeds vs. distance from adult canopies in riparian ("Rip") and slope ("Slp") habitat (site data averaged among years; data for within and away from corridors averaged in riparian sites). No data were available for fallen seeds at 0m in slope habitat. In Spearman's Correlations ( $\alpha = 0.10$ ; p-values multiplied by 6; 1999 data were not included in statistical analysis since no data on fallen fruits were available for this year):  $\rho = -0.72$ ;  $N = 24$ ;  $P = 0.0004$  (fallen riparian seeds);  $\rho = -0.93$ ;  $N = 10$ ;  $P = 0.0005$  (fallen slope seeds);  $\rho = -0.47$ ;  $N = 31$ ;  $P = 0.050$  (processed riparian seeds); and  $\rho = -0.70$ ;  $N = 14$ ;  $P = 0.034$  (processed slope seeds). **(b)** Densities of processed *P. virginiana* seeds oriented along or away from riparian corridors vs. distance from adult canopies in riparian habitat (site data averaged between years). In Spearman's Correlations ( $\alpha = 0.10$ ; p-values multiplied by 6; data from 1999 and from site 4 were not included in statistical analysis since no data away from corridors were available for this year or site):  $\rho = -0.23$ ;  $N = 17$ ;  $P = 1.00$  (seeds along corridor);  $\rho = -0.63$ ;  $N = 17$ ;  $P = 0.038$  (seeds away from corridor). **(c)** Density of processed *P. virginiana* seeds vs. distance from *P. trichocarpa* canopies within corridors of two riparian sites, 1997. In Spearman's Correlations ( $\alpha = 0.10$ ; sites analyzed simultaneously to increase sample size):  $\rho = -0.67$ ;  $N = 8$ ;  $P = 0.069$ .

**Figure 6.** Percent of processed seeds deposited between distances (i.e., at 0m, or >0-0.5m, ... >6.4-15m) from adult canopies for *P. virginiana* plants in riparian and slope habitat (site data averaged among years; data for within and away from corridors averaged in riparian habitat).

**Figure 7.** Number of frugivores departing from *P. virginiana* plants as a function of direction at riparian site 5 (corridor oriented N to S/SE), 1997.



**FIGURE 1**



**FIGURE 2**

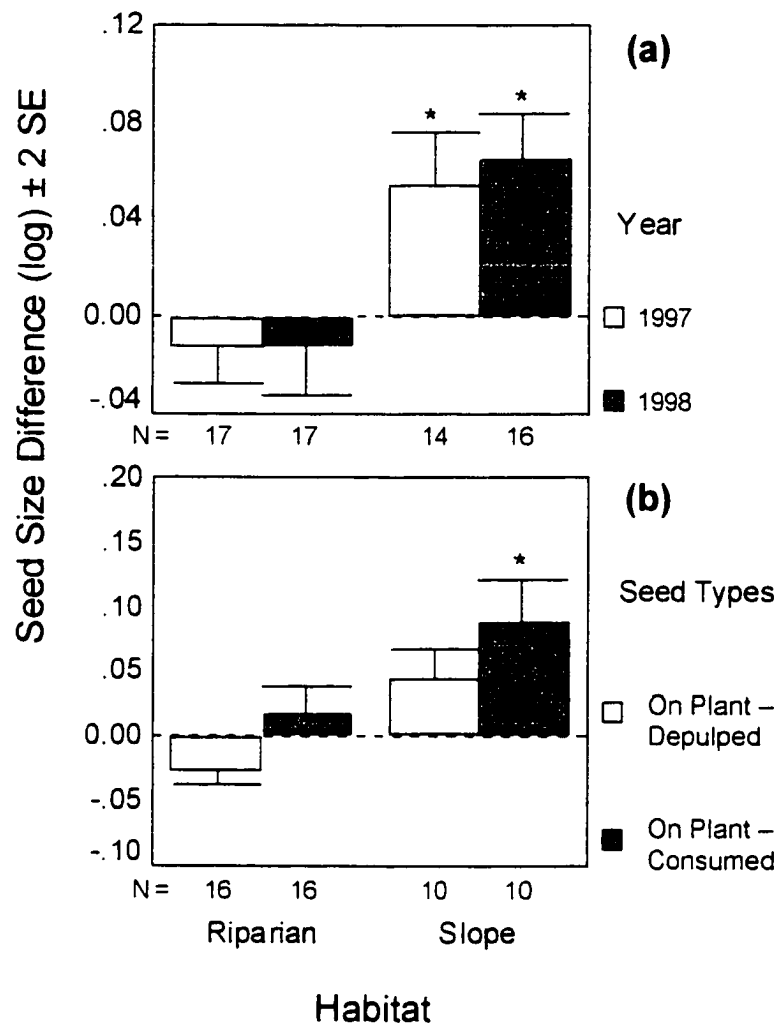
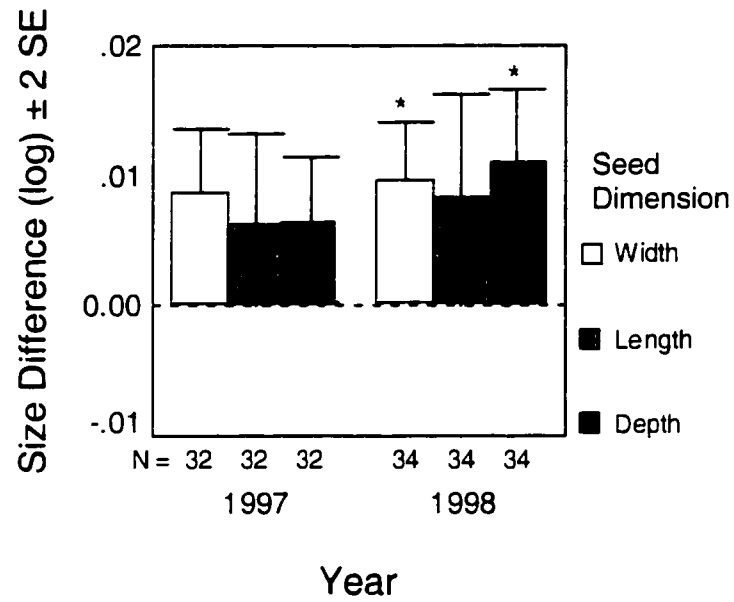


FIGURE 3

**FIGURE 4**

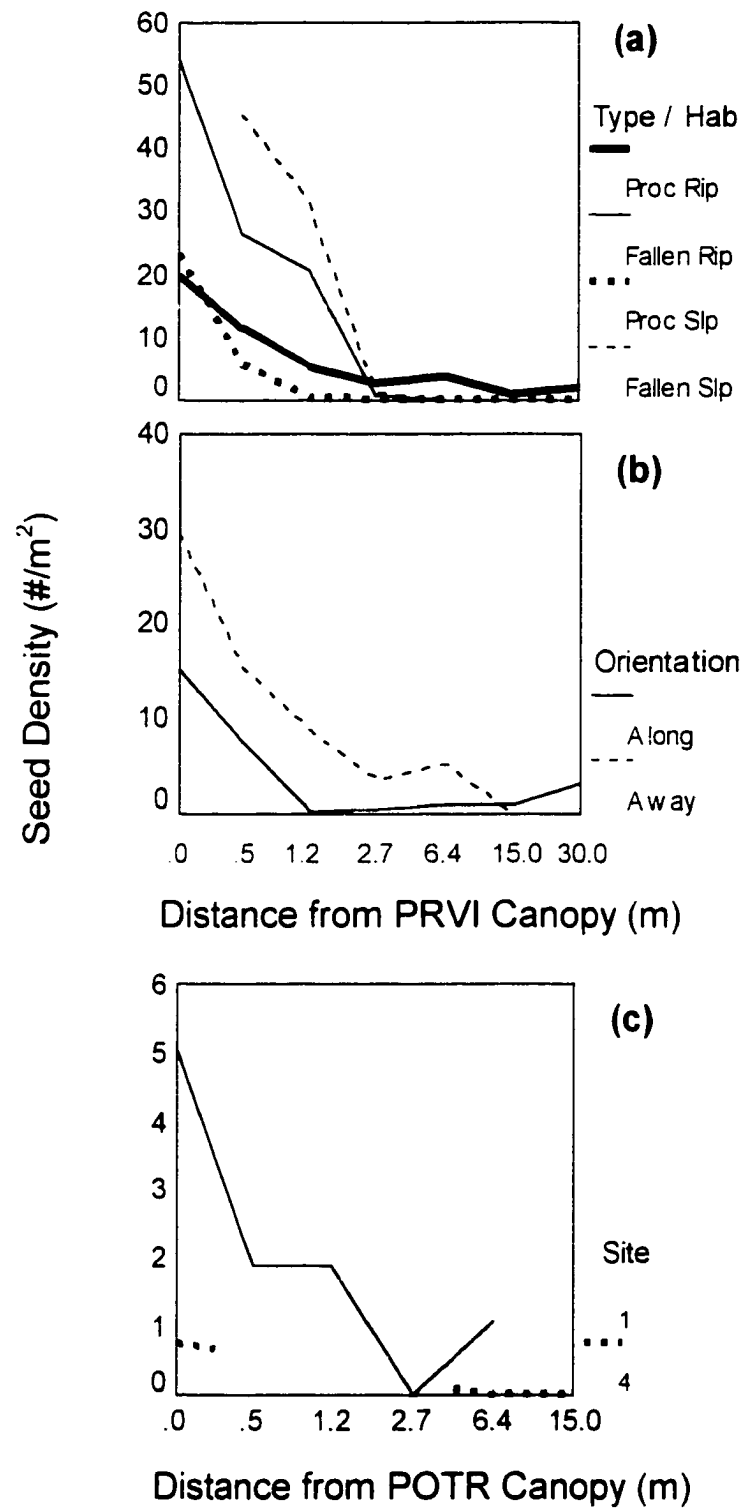
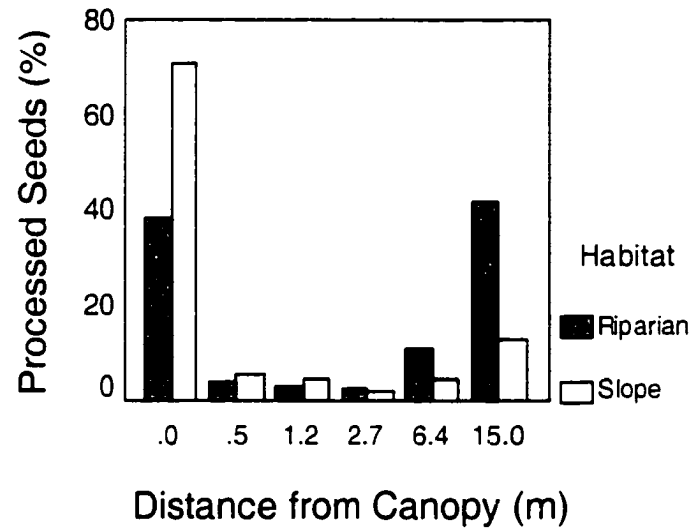
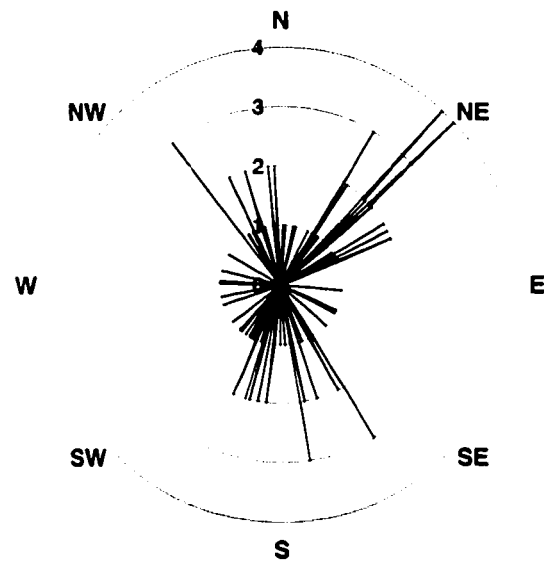


FIGURE 5

**FIGURE 6**

**FIGURE 7**

## **CHAPTER 3**

### **Seed Size, Number and Habitat of a Fleshy-Fruited Plant: Consequences for Seedling Establishment.**



## INTRODUCTION

Mortality of seeds and seedlings is often high relative to that in later stages of plant life cycles, and can have large effects on spatial patterns of plant recruitment and population or community dynamics (e.g., Harper 1977; Connell and Slayter 1977; Keddy 1982; Clark and Clark 1984; Brown and Heske 1990). As a result, mortality factors that are important during this early stage of offspring establishment may impose strong selection pressures on plant reproductive traits such as seed size and number. These traits can influence seed dispersal as well as seed and seedling survival, and can vary widely among and within individual plants (Chapters 1 and 2 and references therein).

Variation in seed size and number may result from tradeoffs between phenotypes that are most advantageous for seed dispersal versus seedling establishment. Plants with large crops of small seeds may experience high dispersal rates, but large seeds from small crops may be more likely to establish successfully once they are on the ground (reviewed in Ch. 1). Conflicts between seed size/number phenotypes also may occur between different stages of offspring establishment, including seed survival and germination, and seedling emergence, survival and growth (Schupp 1995). For example, small seeds escape predation more often than large seeds, but seedlings from large seeds can emerge or survive better than those from small seeds (e.g., Howe et al. 1985; Sork 1987; Vander Wall 1994; Hulme 1998). High densities of seeds or seedlings can increase competition, predation or spread of pathogens, but can also result in predator satiation (e.g., Shaw and Antonovics 1986; Willson and Whelan 1990; Augspurger and Kitajima 1992; Forget 1994; Silva Matos et al. 1999). Ultimately, resolution of these types of conflicts may depend on which stage is most limiting to offspring recruitment.

Selection pressures imposed on seeds and seedlings may differ among environments and contribute to inter- and intra-specific variation in seed size and number (e.g., Webb and Willson 1985; Willson and Whelan 1990; Whelan et al. 1991; Horvitz and Schemske 1995; Hulme 1997; Russell and Schupp 1998). For example, large crops of small seeds may be favored for plants in temporally or spatially unpredictable environments, while small crops of large seeds may be favored in stable but competitive environments (Southwood 1977; Foster 1986; Roff 1992). In addition to environmental predictability, levels of abiotic and biotic stress may have large effects on seedling establishment and thus may be strong drivers of variation in reproductive traits. Plants in abiotically stressful (e.g., resource-limited) environments may benefit from producing small crops of large seeds that result in seedlings capable of surviving despite harsh external conditions (Ch. 1 and references therein). However, reduced dispersal experienced by large seeds can have negative consequences for offspring survival and growth. Seeds that are not dispersed away from parent plants may experience increased predation, pathogen attack, allelopathy or competition with parent plants or siblings (e.g., Janzen 1970; Webb et al. 1967; Connell 1971; Platt 1976; Antonovics and Levin 1980; Augspurger 1983; Webb and Willson 1985; Howe 1993; Kaspari 1993; Barot et al. 1999). Plants in environments with high levels of such biotic stresses thus may enhance fitness by producing large crops of small seeds that are capable of dispersing away from density or distance-dependent mortality factors to more favorable locations. Although many plants occur in environments that vary in levels of abiotic and biotic stress, the differing selective effects of these environments on dispersal versus establishment have not been examined.

This study provides the first comprehensive test of effects of environmental variation in seed size and number on offspring recruitment for *P. virginiana*, an animal-dispersed plant. This species was selected because: **(1)** it exhibits substantial variation in seed size and number between habitats (i.e., large crops of small seeds in mesic riparian habitat, and small crops of large seeds in

xeric slope habitat; Ch. 1), and **(2)** the frugivores that consume and disperse its seeds exhibit distinct preferences with respect to these reproductive traits (Ch. 2). Few studies have connected dispersal patterns created by animals with their consequences for seedling recruitment (Horvitz and Schemske 1994; Chapman and Chapman 1996). Fewer still have examined both the extent and consequences of variation in dispersal-related reproductive strategies for offspring fitness (Howe 1990; Herrera et al. 1994). None of these studies has examined an animal-dispersed plant that exhibits clear variation in reproductive traits between environments that differ in levels of biotic and abiotic stress. The current study presents data from experimental seed and seedling distributions to establish a critical link between plant reproductive strategies and offspring recruitment, and to determine for the first time how and why these strategies vary across environments.

The following hypotheses were tested to determine whether plants resolve the seed size/number tradeoff differently in different environments as a result of the conflict between seed dispersibility and seedling vigor: **(1) Biotic stresses** that occur during seedling establishment may select for production of many small seeds. Biotic stress such as predation should be relatively common in mesic habitat, resulting in high levels of density- or distance-dependent mortality. *P. virginiana* seeds and seedlings are most likely to escape such mortality by dispersal away from conspecific adult plants. **(2) Abiotic stresses** that occur during seedling establishment may select for the production of few large seeds. Abiotic stress such as moisture limitation thus should be relatively common in xeric habitat, and offspring may benefit more from large size than from dispersal away from conspecific adults. For both hypotheses, distinct predictions for each stage of seedling establishment will be stated in the following section.

## STUDY AREA AND METHODS

All tests of *P. virginiana* seed and seedling establishment were conducted in the foothills of the Rocky Mountains of western Montana (~1000m elevation). *P. virginiana* is a shrubby tree that produces fleshy fruits with hardened endocarps (i.e., inner walls) that enclose single seeds until germination. The fruits are particularly attractive to avian frugivores, which consume the fruit pulp and excrete, regurgitate or drop the seeds. Primary frugivores on *P. virginiana* in western Montana are *Bombycilla cedrorum* and *Turdus migratorius* (Parson, pers. obs.). These frugivores remove the greatest numbers of fruits from plants with large fruit crops, and consume (i.e., ingest rather than depulp in place on the plant) relatively small-sized seeds (Ch. 2). Frugivores are likely to have a positive effect on *P. virginiana* seed germination simply by removing the fruit pulp from seeds (Meyer and Witmer 1998). In addition, frugivores that consume seeds may move them away from parent plants to relatively safe sites for seedling establishment. Thus, frugivore preferences may impose current selection pressures on *P. virginiana* to produce large crops of small seeds.

In western Montana, *P. virginiana* typically occurs in two distinct habitat types: scattered in clumps on xeric south to west-facing slopes (generally on exposed, rocky faces), or as part of a continuous band of mesic vegetation on the edges of riparian corridors (Parson, unpubl. data). Densities of potential seed predators (i.e., small mammals) in and near adult *P. virginiana* appear to be higher in riparian than in slope habitat (Parson, pers. obs.). However, abiotic stress may be relatively common in slope habitat because of low levels of soil moisture available to adult plants during the growing season (Ch. 1). In slope habitat, most seeds that are processed (i.e., depulped or consumed) by frugivores are deposited under adult *P. virginiana*. In contrast, most processed seeds in riparian habitat are moved along corridors away from adult *P. virginiana* canopies. Because of the variation in reproductive strategies, dispersal patterns and environments, *P.*

*virginiana* seeds and seedlings are likely to experience markedly different conditions for establishment.

### **Seed Survival**

Once seeds have fallen to the ground, seed survival until germination is a critical first step in successful seedling establishment. The following specific predictions were made about seed survival: If seed predation is relatively high in riparian habitat and seed predators exhibit distance- or density-dependent foraging behavior, seed survival should **(1)** increase with distance from *P. virginiana* canopies in riparian areas but not on slopes, and **(2)** decrease with seed density in riparian areas but not on slopes. If predation is greatest in densely-vegetated or structurally complex areas, **(3)** seed survival should be greater away from rather than along riparian corridors in riparian habitat. If large seeds represent a greater food resource for predators, **(4)** large seeds may be less likely to survive to germination than small seeds, particularly in riparian habitat.

To determine whether seed number and location influence seed survival (**predictions 1-3**) circular plots (i.e., hoops formed from 3 cm-high plastic strips staked to the ground) were placed around adult *P. virginiana*. Plots were established after most natural seed dispersal had ceased in the fall of three consecutive years (1996-1998). Plots were 0.14 m<sup>2</sup> in 1996 and 1997 but were increased to 0.28 m<sup>2</sup> in 1998 to test effects of relatively low densities. Plots were divided between two riparian and two slope sites in 1996 (216 plots total) and three riparian and three slope sites in 1997 and 1998 (324 plots in each year). All riparian sites and two of the slope sites also were used to measure seed dispersal patterns (Ch. 2). Both habitats received the same number of plots, but more plots (i.e., 2 to 5 times as many) were placed in the largest sites within each habitat. Three rows of 3 or 6 plots each (depending on plant size) were placed at 0, 5 and 15 m from the edge of *P. virginiana* canopies, since these distances occurred within the range typical

for *P. virginiana* seed shadows (Ch. 2). At each distance, plots were spaced at least 5 m apart to minimize the chance of interactions between plots. To test the effect of proximity to the riparian corridor (**prediction 3**), plots in the riparian sites were placed in two directions. Specifically, half of the plots at 5 and 15 m extended within the riparian corridor and half extended away from the corridor.

In both habitats, locally-collected viable seeds were placed in the plots at one of three densities (i.e., 22, 144 or 606 seeds/m<sup>2</sup> in 1996 and 1997 and 11, 29 or 71 seeds/m<sup>2</sup> in 1998). All densities occurred within the range documented for *P. virginiana* seed shadows, although densities of seeds processed by frugivores are most often less than 30 seeds /m<sup>2</sup> (Ch. 2). Densities were assigned to plots in a randomized block design across groups of three adjacent plots at each distance, and either within or away from corridors in riparian sites. Seeds were spaced regularly in the plots to simulate dispersal of single seeds, since avian frugivores typically excrete or regurgitate only one *P. virginiana* seed at a time (Witmer, pers. comm.). Seeds in plots were censused every 24 hours until at least one seed or 5% of the seeds (whichever was greater) in one third of the plots in a site was removed by a predator, at which point all of the plots in that site were removed. However, plots still in place after 7 days were removed regardless of total predation.

To test effects of seed size on seed survival (**prediction 4**), sieves were used to separate seeds into two size classes that occurred roughly 1 SD above and below the mean size of naturally-occurring seeds (i.e., 5.9 to 6.35 or 4.45 to 5.0 mm dia.). In the fall of 1998, seeds were placed in 28 plots (i.e., 17.5 cm-dia. plastic dishes; 100 seeds of each size per dish) per habitat within 15m of *P. virginiana* canopies. Plots were checked daily and left in place either for 30 days or until seeds of either size were removed by predators. The numbers of small and large seeds removed by predators were recorded for plots in which any but not all seeds were taken.

*Data Analysis:* An  $\alpha$ -level of 0.05 was used for all tests unless otherwise specified.

Likelihood of plot detection by predators was analyzed in a logistic regression with distance from canopy, habitat, year and all significant two-way interactions as independent variables. However, effect of 1998 seed density was tested with all independent variables except year in a separate logistic regression from the previous two years since different densities were used. In addition, proximity to riparian corridor was tested with all independent variables except habitat in a separate logistic regression for riparian habitat only. Thus, p-values for all logistic regressions were multiplied by 4 to provide a Bonferroni correction for multiple tests. Seed removal rates (i.e., proportion of seeds removed per plot per day) could not be transformed to normal distributions. Thus, associations between removal rates and year, habitat, distance, proximity to riparian corridor (riparian habitat only) and seed density (data from 1998 tested separately from 1996 and 1997 because of different densities used in this year) were analyzed separately in Kruskal Wallis tests; p-values were multiplied by 20 to provide a Bonferroni correction. To test size selectivity by seed predators, paired *t*-tests were used to compare the proportion of small versus large seeds removed per plot.

### **Seed Germination**

Seed germination is the second major step in successful seedling establishment, and may be influenced by seed size as well as differences in light and soil moisture. If low soil moisture levels on slopes limit seed germination, (1) germination should be greater in riparian than in slope habitat. However, if low light levels limit seed germination in densely-vegetated areas, (2) germination should be greater in slope than in riparian habitat, (3) greater away from (versus within) riparian corridors, and (4) greater away from (versus under) *P. virginiana* canopies, particularly in slope habitat. No *a priori* predictions were made about effects of seed size on seed

germination, since previous studies of other species have reported conflicting results (Stanton 1985; Marshall 1986; Stamp 1990).

Effects of seed size and location on seed germination were tested in late fall 1998. Seeds were buried at a depth of 8 mm in 72 plots in riparian habitat (divided equally between sites 2 and 3, above) and 48 plots in slope habitat (divided equally between two of the three sites described above). Plots were located at two distances from *P. virginiana* canopies (i.e., 24 plots at 0 m in each habitat and 48 or 24 plots at 15 m in riparian and slope habitat, respectively). In riparian habitat, half the plots at 15 m were located within the riparian corridor and half were located away from the corridor. In each plot, two mesh bags containing 10 small or 10 large seeds (4.45 to 5.0 or 5.9 to 6.35 mm dia.) were buried just below the soil surface. Bags were removed the following spring (i.e., mid-April) just prior to the time of natural seedling emergence, and number of germinants (i.e., seeds with cracked seed coats and visible radicle tips) was recorded.

*Data Analysis:* To obtain normally-distributed variables for statistical analysis, the proportions of small and large-sized seedlings that germinated per plot were arcsine-square root transformed.

Effects of habitat and distance on seed germination were examined in a Simple Factorial ANOVA (habitat \* distance interaction was not included in the model because it was not significant).

Effect of proximity to riparian corridors on seed germination was examined for plots at 15 m in a separate Simple Factorial ANOVA (riparian habitat only). Thus, p-values were multiplied by 2 for both ANOVA's to provide a Bonferroni correction. Effects of seed size on seed germination were analyzed in paired samples *t*-tests for each habitat; p-values were multiplied by 2 to provide a Bonferroni correction.



**Seedling Emergence, Survival and Growth**

The emergence, survival and growth of germinated seeds represent the final stages in successful offspring recruitment. If low levels of soil moisture increase the risk of seedling desiccation in open, unshaded areas, (1) seedling establishment (i.e., emergence, survival and growth) should be greater in riparian than in slope habitat, and (2) greater under versus away from *P. virginiana* canopies in slope habitat. If seedling predation is relatively high in riparian habitat and predators exhibit distance- or density-dependent foraging behavior, (3) seedling survival and growth should increase with distance from *P. virginiana* canopies or away from corridors in riparian habitat, and (4) decrease with seedling density in riparian areas but not on slopes. If the heavier endosperm tissue of large versus small *P. virginiana* seeds (Ch. 1) provides large seeds with more resources for early growth, (5) large seeds should be more likely to establish as seedlings than small seeds, but (6) this size benefit may only occur in severely resource-limited areas (i.e., away from *P. virginiana* canopies in slope habitat).

Because the above comparisons provide only correlational evidence that specific factors influence seedling establishment, the following additional predictions were experimentally tested: If predation negatively affects seedling growth and survival and seed dispersal allows seedlings to escape predation in riparian habitat, (7) seedling establishment should be greater in plots protected from mammalian predation than in unprotected plots, especially (8) under *P. virginiana* canopies in riparian habitat. If large seeds are produced on slopes because they benefit seedlings in low moisture conditions, (9) seedlings should experience lower soil moisture levels on slopes than in riparian areas; and (10) advantages of large seeds for seedling establishment should be especially apparent in dry, infrequently-watered soil.

Location and density effects on seedling establishment (**predictions 1-4**) were tested by sowing locally-collected, germinated seeds in the same riparian and slope sites that were used for seed

germination tests. During three consecutive springs (1997-1999), germinants were planted 8 mm deep in plots that were located at the same three distances used for the seed survival experiment (see above). Plots were 0.13 m<sup>2</sup> in 1997 and 1998 but were increased to 0.25 m<sup>2</sup> in 1999 to test effects of relatively low densities. In riparian sites, half of the plots at 5 and 15 m extended within the riparian corridor and half extended away from the corridor. In all years, more plots (i.e., 1.5 to 2 times as many) were placed in the largest sites within each habitat. A total of 121 plots were established in 1997 (61 in riparian and 60 in slope habitat), 114 plots in 1998 (59 in riparian and 54 in slope habitat), and 130 plots in 1999 (76 in riparian and 54 in slope habitat).

In both habitats, germinants were planted at each of three densities in 1997 (i.e., 38, 154 or 646 germinants/m<sup>2</sup>) or at each of two densities in 1998 (i.e., 123 or 377 germinants/m<sup>2</sup>) and 1999 (i.e., 56 or 140 germinants/m<sup>2</sup>). Densities were assigned to plots in a randomized block design similar to the seed survival experiment (above). However, densities of emerged seedlings were not always correlated with initial densities of germinants because of microhabitat effects. To control for these effects, seedlings were thinned once they emerged to pre-assigned "low" or "high" densities that occurred within the range documented for *P. virginiana* seed shadows. In 1997, seedlings were not thinned, so effects of density in this year were not analyzed. In 1998, emerged seedlings in low-density plots were thinned to a maximum of 38/m<sup>2</sup> ( $\bar{x} = 23/\text{m}^2$ ), and seedlings in high-density plots were excluded from analysis if there were fewer than 77/m<sup>2</sup> ( $\bar{x} = 131/\text{m}^2$ ). In 1999, emerged seedlings in low-density plots were thinned to a maximum of 12/m<sup>2</sup> ( $\bar{x} = 12/\text{m}^2$ ), and seedlings in high-density plots were excluded from analysis if there were fewer than 60/m<sup>2</sup> ( $\bar{x} = 64/\text{m}^2$ ).

To supplement the number of plots in which seedlings survived past the cotyledon stage, seedlings rather than germinants were planted in 42 additional 0.13 m<sup>2</sup> plots in 1998 and in 80 additional 0.25 m<sup>2</sup> plots in 1999. Seedlings planted in these plots germinated at the same time as the previously-described germinants, but were raised in containers outside (in a soil mixture collected from both habitats) for one additional month before being planted in the field. In 1998, 20 plots were placed in one slope site (10 plots each at 0 and 15 m) and 22 plots in one riparian site (9 plots at 0 m, 11 plots at 15 m within the corridor, and 2 plots at 15 m away from the corridor; most plots were located along the corridor since this location was in greatest need of supplementation). In 1999, plots were located at same sites and distances used for plots with germinants (resulting in 50 plots in riparian and 30 in slope habitat; 1.5 times as many plots were placed in the largest site within each habitat). In both years, plots in sites at each distance were randomly assigned one of two seedling densities (23 or 77 /m<sup>2</sup> in 1998 and 12 or 60 /m<sup>2</sup> in 1999). Results for these plots were combined with results for plots in which germinants were planted, since between-habitat differences in survival were similar for both methods of planting.

To test effects of seed size on seedling establishment (**predictions 5-6**), seeds were separated into 3 size classes that spanned the range of naturally-occurring sizes (i.e., < 5.3, 5.6-5.9 and > 6.35 mm dia.). Average seed size of riparian plants ( $\bar{x} \pm 1 \text{ SD} = 5.45 \pm 0.43 \text{ mm dia.}$ ; Ch. 1) occurred between the small and medium experimental sizes, while average seed size of slope plants ( $\bar{x} \pm 1 \text{ SD} = 5.99 \pm 0.49 \text{ mm dia.}$ ; Ch. 1) occurred between the medium and large experimental sizes. During three consecutive springs (1997-1999), locally-collected germinated seeds were sown 8 mm deep in the two riparian and two slope sites used for seed germination tests. Plots in each site were placed at two distances (i.e., under or 15 m away from adult *P. virginiana* canopies). In 1997 and 1998, 120 plots were divided equally among all sites and distances (all plots at 15 m in riparian sites were oriented away from the corridor). However, 30 additional plots were located

in one riparian site in 1997 (divided equally between distances) and 1 additional plot was established at 15 m in slope habitat in 1998. In 1999, 150 plots were established, with the 30 additional plots placed at 15 m along the corridor of the two riparian sites to allow tests of the effect of proximity to the riparian corridor. At each distance, plots were placed in groups of three, and each plot in a group contained six germinants from one of the three size classes (because of limited seed supply, only five germinants/plot were planted in 1999). Plots were covered with 9 cm dia.  $\times$  30 cm high  $\times$  1.3 cm mesh hardware cloth cylinders that were fastened to the ground and closed at the top to minimize damage by mammalian predators.

To isolate effects of predation and moisture deficits on seedling establishment, additional plots were established in the seed size experiment in spring 1999. For the predation experiment (**predictions 7-8**), 50 plots were established that were similar in size and location to the seed size plots (above) but without predator exclosures. Each plot was planted with five germinants from medium-sized (5.6-5.9 mm dia.) seeds, and was located approximately 1 m from one of the 50 otherwise identical protected plots. For the soil moisture experiment (**predictions 9-10**), germinants from three sizes of seeds (above) were planted in 75 protected plots identical in design and distance to the seed size plots (above). Plots were located in riparian site 2 (45 plots) and in one of the previously-used slope sites (30 plots) at least 5m away from the original (i.e., "control") seed size plots. The new plots received supplemental water three days per week throughout the growing season. During each watering period, water was applied to all plots in the amount necessary to saturate the soil to a depth of 6 cm (i.e., approximate length of *P. virginiana* roots after one growing season). In addition, a pressure bomb was used to measure pre-dawn seedling water potentials (MPa) of naturally-occurring seedlings in mid-July, 1999. Ten field-grown *P. virginiana* seedlings (i.e., 13-month-old seedlings that had been planted at one month of age in 1998) each were sampled in one riparian and one slope site. Seedlings were sampled

equally at 0 or 15 m from adult *P. virginiana* canopies. All sampling was performed from 3:00 A.M. to 6:00 A.M. in dry conditions.

For all plots, seedling emergence and survival were censused every one (1998 and 1999) or two weeks (1997) for three months. For the duration of the 1998 and 1999 census periods, the primary causes of seedling mortality (e.g., predation, root rot and desiccation) were determined if possible. For seedlings in the seed size experiment (1998 and 1999 only), height and leaf area of all leaves (1998) or of the largest two leaves (1999) were measured twice during the growing season. When seedlings were approximately 10 weeks (all 1999 experiments) or 13 months old (1997 and 1998 seed size experiments), they were harvested, dried at 60° C for three days, separated into above- and below-ground biomass and weighed.

*Data Analysis:* To obtain normally-distributed variables for statistical analysis, the proportion of seedlings that emerged (in seedling location plots) was arcsine-square root transformed, rates of growth in height, leaf area (seed size plots) and mass (seed size plots) were square-root transformed, and number of leaves (1999 seed size plots) and average root:shoot mass ratios per plot (seedling location and 1999 seed size plots) were log<sub>10</sub> transformed. Tests of variables that could not be transformed to normal distributions were nonparametric.

For the seedling location plots, effects of distance, habitat, year and all significant two-way interactions on proportion of seedlings emerged/plot were analyzed in General Factorial ANOVA's. For location plots in riparian habitat, effect of proximity to riparian corridor on emergence was tested with all fixed effects in a separate ANOVA. To provide a Bonferroni correction, p-values were multiplied by 2 for both tests. Associations between percent seedlings survived/plot and density, distance, habitat, year or proximity to riparian corridor were analyzed separately in Kruskal Wallis tests; p-values were multiplied by 18 to provide a Bonferroni correction. Associations between year (1998 and 1999 only), habitat and the percent of seedlings

that died as a result of predation or desiccation (i.e., the two primary mortality factors; Parson, unpubl. data) were tested in Wilcoxon Signed Ranks Tests; p-values were multiplied by 4 to provide a Bonferroni correction. Associations between average root:shoot ratios/plot (1999 only) and habitat, distance, density, proximity to riparian corridor and all significant two-way interactions were analyzed in two General Factorial ANOVA's. Average above + belowground seedling mass/plot could not be transformed to a normal distribution and was analyzed in six Kruskal-Wallis tests. Thus, p-values were multiplied by 8 for tests of both mass and root:shoot ratios to provide a Bonferroni correction.

For protected plots that did not receive supplemental water, the effect of seed size on emergence was analyzed in a General Factorial ANOVA (with year, habitat, distance and all significant two-way interactions as additional factors). Proximity to riparian corridor was tested separately for 1999 riparian plots, so p-values were multiplied by 2 for both tests to provide a Bonferroni correction. However, results were not significant and are not presented below. Effects of seed size on seedling survival were analyzed in Kruskal-Wallis tests for each habitat/year combination; p-values were multiplied by 6 to provide a Bonferroni correction. Multivariate ANOVA's were used to analyze effects of seed size on seedling growth (i.e., mm increase in height and leaf area/day, number of leaves, mg increase in total mass/day and root mass:shoot mass ratios; data for individual seedlings within plots was averaged). In these tests, habitat, distance, seed size and all significant two-way interactions were included as fixed effects. Because methods for measuring leaf area differed between 1998 and 1999 and mass and root:shoot ratios were only measured in 1999, these years were tested separately. Thus, p-values were multiplied by 2 to provide a Bonferroni correction. Early and late growth rates (i.e., height and leaf area measured between emergence and 1 week, and between 1 and 4 weeks, respectively) were included as separate variables in these analyses because they differed in multivariate repeated measures ANOVA's (1998:  $F_{2, 88} = 1453.75$ ;  $P < 0.0005$ , and 1999:  $F_{2, 70} = 391.10$ ;  $P < 0.0005$ ). In

addition, seedlings with substantial cotyledon damage (i.e., greater than 25% of total cotyledon area removed by predators) were not included in analyses of growth. Effects of seed size on average mass and number of leaves of 1-year old seedlings (planted in 1997 and 1998) were tested with General Factorial ANOVA's (in which year, habitat, distance and all significant two-way interactions were included as fixed effects). Separate tests were used for mass and number of leaves since data for number of leaves were only available for seedlings planted in 1998. In addition, effects of seed size on root:shoot ratios of 1-year old seedlings were tested in Kruskal-Wallis tests for each habitat/year combination. Thus, p-values were multiplied by 6 for all tests of growth of 1-year-old seedlings to provide a Bonferroni correction.

For the soil moisture experiment and seed predation experiments,  $\alpha$ -levels were increased to 0.10 because of small sample sizes. General Factorial ANOVA's were used to analyze associations between seedling emergence and water treatment or protection from predators (other fixed effects included habitat, distance, seed size in the soil moisture experiment, and all significant two-way interactions). Kruskal-Wallis tests were used to examine the association between seedling survival and water treatment. One test was conducted per habitat but additional tests of water effects were conducted for each habitat/seed size combination; thus, p-values were multiplied by 8 to provide a Bonferroni correction. Similarly, Kruskal-Wallis tests were used to examine the association between survival and protection from predators (because one test was conducted per habitat, p-values were multiplied by 2 to provide a Bonferroni correction). Effects of water or predator protection treatment on seedling growth (described above for seed size experiment) were analyzed in Multivariate ANOVA's. In these tests, habitat, distance, seed size (soil moisture experiment only), treatment effect and all significant two-way interactions were included as fixed effects.

Kruskal-Wallis tests ( $\alpha = 0.10$ ) were used to compare seedling xylem pressure potentials between habitats and between distances within habitats. Thus, p-values were multiplied by 3 to provide a Bonferroni correction.

## RESULTS

### Seed Survival

Detection of *P. virginiana* seeds by mammalian predators varied among years and with distance from *P. virginiana* canopies, but the effect of distance varied with habitat. More plots were detected in 1996 than in the subsequent two years, particularly in riparian habitat (Fig. 1a). In all years, detection was greater underneath than 5 or 15 m away from *P. virginiana* canopies, but only in riparian habitat (Fig. 1b). In addition, plots oriented along riparian corridors were detected more than plots located away from corridors (Fig. 1c). In both habitats, high densities of seeds were more likely to be detected than low densities in 1996 and 1997 (Deviance, or change in  $-2 \log$  likelihood if each covariate is removed individually from the model = 9.63;  $N = 540$ ;  $P = 0.032$ ) and marginally so in 1998 (Deviance = 8.75;  $N = 324$ ;  $P = 0.052$ ).

Once plots were detected by predators, large amounts of seeds were removed (median percent seed removal per detected plot = 98% in riparian habitat and 95% in slope habitat). Seeds were removed faster in riparian than slope habitat in 1997 ( $X^2 = 15.31$ ;  $N = 162$ ;  $P = 0.0018$ ) but not in 1996 ( $X^2 = 0.64$ ;  $N = 203$ ;  $P = 1.00$ ) or 1998 ( $X^2 = 6.01$ ;  $N = 152$ ;  $P = 0.28$ ). Rates of seed removal varied among years in riparian but not slope habitat (Table 1). Unlike plot detection, rates of seed removal in riparian habitat were greater in 1998 than in 1996 and 1997 (Fig. 2a). Similar to plot detection, seed removal was associated with distance from *P. virginiana* canopies, but again only in riparian habitat (Fig. 2b). However, the effect of distance was only significant



in 1998, when the rate of seed removal was higher under canopies than 5 or 15 m away from canopies (Table 1). Seed density and orientation with respect to riparian corridors did not influence seed removal (Table 1). In both habitats, more large seeds were removed by predators than small seeds (Fig. 3).

### **Seed Germination**

Seed germination was greater in slope than riparian habitat ( $F_{1, 225} = 6.49$ ;  $P = 0.024$ ), but did not vary with proximity to riparian corridors ( $F_{1, 86} = 0.96$ ;  $P = 0.66$ ), or with distance from *P. virginiana* canopies ( $F_{1, 225} = 0.97$ ;  $P = 0.66$ ). Seed size did not influence seed germination in either riparian ( $t = 2.22$ ;  $df = 67$ ;  $P = 0.06$ ) or slope habitat ( $t = 0.38$ ;  $df = 45$ ;  $P = 1.00$ ).

### **Seedling Emergence, Survival and Growth**

#### *Seedling Location:*

In the seedling location plots, emergence was low and did not differ between riparian and slope habitats ( $F_{1, 330} = 3.06$ ;  $P = 0.16$ ) or among years ( $F_{2, 330} = 2.98$ ;  $P = 0.10$ ). In all years, emergence decreased with distance from *P. virginiana* canopies in slope habitat, but did not vary with distance in riparian habitat (Fig. 4a). Seedling emergence was greater away from rather than along riparian corridors in 1998 (Fig. 4b).

For plots in which seedlings emerged, similar proportions of seedlings survived in riparian and slope habitats in 1997. However, seedling survival was greater in slope habitat in 1998 and greater in riparian habitat in 1999 (Fig. 5a). Seedling survival also varied strongly among years in both habitats (Table 2). Seedling survival increased with distance from *P. virginiana* canopies in riparian habitat in 1998 (Table 2; Fig. 5b). In contrast, survival decreased with distance from

*P. virginiana* canopies in slope habitat, but only in 1999 (Table 2; Fig. 5c). Survival did not vary with seedling density or with proximity to riparian corridors (Table 2).

The importance of primary causes of seedling mortality (i.e., predation and desiccation) in the seedling location experiments varied between habitats and years. In 1998, more seedlings in riparian habitat died as a result of predation than desiccation, while similar proportions of seedlings died as a result of predation and desiccation on slopes (Fig. 6a). In 1999, similar proportions of seedlings died as a result of predation and desiccation in riparian habitat, while more seedlings died as a result of desiccation than predation on slopes (Fig. 6b).

In the 1999 location experiment, average seedling mass/plot was greater in riparian habitat than on slopes ( $X^2 = 8.55$ ;  $N = 70$ ;  $P = 0.028$ ). Mass increased slightly (but not significantly) with distance in riparian ( $X^2 = 7.34$ ;  $N = 44$ ;  $P = 0.054$ ) but not slope habitat ( $X^2 = 0.25$ ;  $N = 26$ ;  $P = 1.00$ ). Mass did not vary with seedling density or with proximity to riparian corridors ( $P = 1.00$  for all tests). Seedling root:shoot ratios did not vary with habitat, distance or density ( $F_{1,94} = 1.29, 0.34, 0.036$ , respectively;  $P = 1.00$  for all factors), or with proximity to riparian corridors ( $F_{1,43} = 0.43$ ;  $P = 1.00$ ).

#### *Seed Size:*

Seedling emergence in the protected, unwatered seed size plots varied with seed size, as well as with year and habitat. Medium-sized seeds emerged more than small seeds in slope habitat (Fig. 7). Emergence was greater in riparian habitat than on slopes ( $F_{1,414} = 25.75$ ,  $P < 0.0005$ ), and greater in 1998 than in 1997 or 1999 ( $F_{2,414} = 6.93$ ,  $P = 0.0022$ ). However, interactions between seed size and habitat or year were not significant. In addition, seed size did not influence seedling survival in either habitat or in any year ( $P > 0.95$  for all tests).

Seed size was positively associated with leaf area growth in 1998 (Table 3). Effects of seed size \* habitat interactions on seedling growth were not significant. However, 1999 seed size was weakly positively associated with height growth and number of leaves in slope but not riparian habitat (Fig. 8). In 1999, seed size did not influence root:shoot ratios or overall rates of growth (i.e., mg/day), but the Bonferroni correction applied to tests of these variables was conservative (since mass and root:shoot ratios were not included in the MANOVA for 1998 seedling growth). In fact, seed size was weakly positively associated with overall growth rates in both habitats (Fig. 9a). For 13-month-old seedlings, seed size was positively associated with overall growth rates, particularly in slope habitat (Fig. 9b). Root:shoot ratios and number of leaves at 13 months did not vary with seed size ( $P > 0.10$  for all tests).

#### *Seed Size\*Water:*

Although the provision of supplemental water increased seedling emergence in slope habitat (Fig. 10a), water treatment did not interact with seed size to influence emergence. Water also was positively associated with seedling survival in slope but not riparian habitat (Fig. 10b), but survival of seedlings from medium and large seeds did not differ between water treatments. However, seedlings from small seeds were less likely to survive in unwatered than watered plots in slope habitat (Fig. 11). Supplemental water was positively associated with all aspects of seedling growth (except root:shoot ratios) in slope but not riparian habitat (however, individual variables were not significant in univariate tests; Table 4). Seed size was positively associated with number of leaves and overall rates of growth (i.e., mg/day; Table 4), but did not interact with water treatment to influence seedling growth.

#### *Seedling Protection:*

Protection of seedlings from mammalian predators did not influence seedling emergence ( $F_{1,96} = 0.063$ ;  $P = 0.80$ ) or survival in riparian ( $X^2 = 3.56$ ;  $N = 59$ ;  $P = 0.12$ ) or slope habitat ( $X^2 = 2.70$ ;

$N = 37$ ;  $P = 0.20$ ). In addition, protection did not influence seedling growth in either habitat (Table 5). This experiment may have failed to find effects of protection because the predator exclosures did not completely exclude predators (Parson, pers. obs.).

#### *Soil Water Availability:*

Seedlings on slopes experienced lower soil moisture levels than seedlings in riparian areas, but soil moisture did not vary with distance from *P. virginiana* canopies in either habitat (Fig. 12).

## DISCUSSION

Patterns of *P. virginiana* seed and seedling establishment demonstrate that environmental conditions can have strong effects on offspring recruitment. Differences between slope and riparian habitats directly influenced every stage of recruitment, from the survival of recently-dispersed seeds to the growth of established seedlings. Variation in the distance-dependence of seed and seedling stages was particularly noticeable between habitats. In riparian habitat, seed and seedling survival and overall growth rates were positively associated with distance from adult *P. virginiana* canopies. In contrast, seedling emergence and survival were negatively associated with distance from *P. virginiana* canopies in slope habitat. Although location of seeds or seedlings influences offspring establishment of many species, the relationship between distance from conspecific adults and offspring establishment has only rarely been reported to be negative (Fuentes et al. 1986; Debussche and Isenmann 1994; Russell and Schupp 1998; Weltzin and McPherson 1999), and has never been reported to vary between negative and positive within a single species.

**Distance and Density-Dependent Effects on Seedling Establishment**

Distance-dependent effects on offspring establishment have large implications for the relative importance of seed dispersal. Positive distance dependence (i.e., increased offspring establishment with distance from parent plants), such as occurred for riparian *P. virginiana*, may place relatively high selection pressure on plants to disperse their seeds (Howe and Smallwood 1982; Augspurger 1984; Dirzo and Dominguez 1986; Howe 1990 and references therein; Willson 1992; Barot et al. 1999). Seed survival also was greater away from versus along riparian corridors, suggesting that vegetation structure as well as distance plays an important role in offspring establishment (Mittelbach and Gross 1984; Gill and Marks 1991; Myster and Pickett 1993; Diaz et al. 1999). Negative distance dependence (i.e., decreased offspring establishment with distance from parent plants), such as occurred for slope *P. virginiana*, may result in little or no selection pressure on plants to disperse their seeds. In fact, plants in these environments may benefit more in the short term by *not* dispersing their seeds (similar to plants in desert environments; Ellner and Shmida 1981).

Effects of offspring density on establishment also may influence the relative importance of dispersal because of the reduction in seed density that is associated with dispersal (Janzen 1970; Connell 1971, 1979; Clark and Clark 1984; Willson 1992). For high *P. virginiana* seed densities (i.e., 1997 and 1998 experiments), a negative association occurred between density and detection by predators on slopes as well as in riparian habitat. This pattern does not support the hypothesis that greater density-dependence should occur in the habitat with greater predation pressure (i.e., riparian habitat). Instead, plants in both environments may experience selection pressure to avoid offspring predation by dispersing seeds. However, high seed predation pressure in riparian habitat (in some years) may exert proportionally higher pressure on riparian plants than on slope plants to reduce seed densities. Because of high seed dispersal in riparian habitat, seeds were

deposited under *P. virginiana* canopies by frugivores at a relatively low density ( $\bar{x} \pm 1 \text{ SD} = 20.0 \pm 11.3 \text{ seeds/m}^2$ ; Ch. 2). This density was similar to the low (1996 and 1997) and medium (1999) density treatments used in the seed survival experiment. For these treatments, negative effects of seed density on seed survival were not apparent. In slope habitat, seeds also were deposited under canopies by frugivores at a low density ( $\bar{x} = 23.3 \pm 15.7 \text{ seeds/m}^2$ ), but dispersal away from canopies was low as well (Ch. 2). Thus, current high rates of dispersal in riparian but not slope habitat may be an adaptive response to density-dependent seed predation pressure.

### **Seed Size: Direct Effects on Seedling Establishment**

Seed size can have strong direct effects on seedling establishment, in addition to indirect effects through its influence on seed dispersal patterns (e.g., Ch. 2; Dolan 1984; Morse and Schmitt 1985; Winn 1988; Turnbull et al. 1999). The relatively large size of *P. virginiana* seeds on slopes decreases chances of consumption by frugivores (Ch. 2), but may increase chances of seedling establishment. Specifically, greater cotyledon reserves may allow large seeds to develop longer radicles faster and establish in relatively extreme abiotic conditions (i.e., low levels of soil moisture). Seed size effects are particularly common in environments where resources such as soil moisture or light are limited (Platt 1976; Howe et al. 1985; Wulff 1986; Gross and Smith 1991; Manga and Yadav 1995). *P. virginiana* seed size positively influenced rates of seedling leaf growth in both habitats (Table 3), but other advantages of large seeds were only apparent in the relatively dry slope habitat. In this habitat, seedlings from medium-sized seeds were more likely to emerge than those from small seeds (Fig. 7). In addition, seedlings from large seeds on slopes grew taller faster, produced more leaves and were heavier overall than those from small seeds (Figs. 8 and 9). In the soil moisture experiment, the disadvantage of small seeds was evident when seedlings did not receive supplemental water, but only in slope habitat (Fig. 11).

Thus, the importance of relatively large seeds for seedling establishment on slopes may override the negative effect on the likelihood of consumption by frugivores.

The relatively small size of seeds in riparian habitat suggests that resource limitations are less severe and predation pressure more severe in this environment. Because seed germination was lower in riparian than in slope habitat, light rather than moisture levels may limit this early stage of seedling establishment. However, seed germination and seedling survival and growth were not greater away from versus along the densely-vegetated riparian corridors. In addition, small seeds may have benefited rather than hindered seedling establishment in the relatively benign riparian environment. Small seeds germinated in greater proportions than medium and large-sized seeds in optimal greenhouse conditions (Parson, unpubl. data). This pattern was weak in natural conditions, and only occurred in riparian habitat. However, the largest direct benefit of small seeds for seedling establishment most likely resulted from the negative association between seed size and seed survival. The increased chance of escape from predation of small seeds supports the hypothesis that large seeds are more attractive to predators (Mittelbach and Gross 1984; Podolsky and Price 1990; Boman and Casper 1995). Overall, seed predation was greatest in riparian corridors (Fig. 1c), and may have placed substantial pressure on seeds to be small in this environment.

The strengths of direct seed size effects on establishment may be compared by examining probabilities of successful transition from dispersed seeds to established seedlings (Fig. 13). Riparian plants with small seeds experienced a 31.9% increase in seedling establishment relative to plants with large seeds. This increase occurred due to greater survival of small seeds than large seeds. In contrast, slope plants with large seeds experienced a 4.2% increase in establishment relative to plants with small seeds. This increase occurred due to slightly greater emergence of seedlings from large seeds than from small seeds. However, this estimate of the benefit of large

seeds is conservative because effects of seed size on seedling growth were not included.

Large positive effects of seed size on seedling growth in slope habitat (e.g., Fig. 9b) may result in a strong net fitness advantage for seedlings from large seeds.

### **Relative Importance of Seed Dispersal versus Seedling Establishment**

To my knowledge, the results for *P. virginiana* seeds and seedlings (Ch. 2 and current study) provide the first evidence that a tradeoff between the importance of dispersal and establishment for a single species varies with environment. In addition, environmental factors that influence offspring establishment appear to be mediated by the indirect effects of plant reproductive strategies on seed dispersal patterns. For example, establishment in riparian habitat was positively distance-dependent, but not all seeds were dispersed away from parent plants (Ch. 2). Thus, dispersal may be one of the primary limiting factors to offspring recruitment in this environment. Most *P. virginiana* seeds were dispersed relatively long distances in riparian habitat, most likely because of an abundance of potential perch sites and the consistent production of large crops of small seeds (Ch. 2). The advantage of the riparian *P. virginiana* dispersal strategy is apparent when probabilities of transition are examined for the dispersal and establishment stages of offspring recruitment (Fig 14a). These patterns indicate that the production of large crops of small seeds in riparian habitat may be an adaptive response of plants to enhance seed dispersal. In turn, this dispersal allows seeds to escape to more suitable locations for seedling recruitment.

On slopes, offspring establishment was negatively distance-dependent in some years, and was never positively associated with distance. In addition, seeds processed by frugivores were deposited primarily under *P. virginiana* canopies, most likely because of the scarcity of other perch sites and the consistent production of small crops of large seeds (Ch. 2). In this habitat, as



in riparian habitat, the majority of seeds on slopes were deposited in the microsites most suitable for seedling establishment (Fig. 14a). This pattern may occur because *P. virginiana* on slopes function as nurse plants to their offspring, similar to bird-dispersed shrubs in dry areas of the Chilean matorral (Fuentes et al. 1984, 1986). Specifically, slope plants may facilitate seedling establishment by ameliorating harsh physical conditions and protecting seedlings from desiccation (caused by low soil moisture, high-temperatures or high light intensity; Callaway 1995 and references therein; Holmgren et al. 1997; Weid and Galen 1998; Weltzin and McPherson 1999). As a result, seed dispersal to appropriate microhabitats may not be as limiting as offspring establishment in this environment. Because of the benefits of large seeds in low-moisture conditions, the production of small crops of large seeds by slope *P. virginiana* appears to be an adaptive response of plants to enhance seedling establishment.

The change in parent-offspring interactions from negative to positive between riparian and slope habitat provides partial support for the competition/facilitation hypothesis of Bertness and Callaway (1994; see also Callaway and Walker 1997). According to this hypothesis, competitive and other negative interactions should predominate between plants in physically benign, productive environments. However, positive interactions should become increasingly important in abiotically stressful environments. Although facilitation of seedling emergence or survival by adult plants is common (Suding and Goldberg 1999 and references therein), facilitative effects of conspecific adults on offspring have rarely been documented (but see Weid and Galen 1998 and references therein; Weltzin and McPherson 1999). In addition, conspecific facilitation has not been documented for fleshy-fruited woody plants and their offspring. Specific facilitative effects of adult *P. virginiana* on offspring were not tested, but parent plants may function by alleviating moisture limitations for the following reasons: (1) mortality on slopes as a result of desiccation was relatively high (Fig. 6), (2) soil moisture was particularly limited for slope seedlings (Fig. 12), and (3) slope seedlings responded strongly and positively to water supplementation (Fig. 10).

Ultimately, facilitation by *P. virginiana* adults may reduce selection pressure for seed dispersal, although interactions between adults and offspring may change as offspring age and begin to compete with larger plants (e.g., McAuliffe 1984; Bertness and Yeh 1994; Berkowitz et al. 1995).

### **Temporal Variation in Offspring Establishment**

Within habitats, substantial variation occurred in patterns of offspring establishment among years. Such temporal variation is common, and may have large consequences for the evolution of reproductive strategies (e.g., Capinera 1979; McGinley 1987; Schupp 1988a; Whelan et al. 1991; Venable and Brown 1998; Germaine and McPherson 1999). Much of the variation in *P. virginiana* establishment may have resulted from variation in levels of precipitation during seedling emergence and early seedling growth. During these stages, seedlings have limited root systems and are particularly susceptible to moisture limitation. Proximity to riparian corridors, for example, influenced seedling emergence only in 1998, when emergence was greater away from rather than along riparian corridors. In 1998, levels of precipitation were high during the months seedlings were growing actively (i.e., May through July;  $\bar{x} \pm 1 \text{ SD} = 9.47 \pm 1.37$  cm/month) relative to the 30-year average ( $3.78 \pm 1.28$  cm/month; data from the Western Regional Climate Center Web Page). In contrast, levels of precipitation were average in 1997 ( $4.66 \pm 0.95$  cm/month) and 1999 ( $3.42 \pm 3.50$  cm/month). Orientation away from corridors thus may be beneficial for seedling emergence (e.g., by reducing competition for light), but only in relatively wet years when this location receives adequate moisture (Hubbard and McPherson 1999). In addition, seedling survival in slope habitat was relatively high in 1998 (Fig. 5a), and did not decline with distance from *P. virginiana* canopies as it did in 1999 (Figs. 5b and c). In western Montana, el Niño years such as 1998 occur at intervals of 3 to 7 years, and are associated

with greater than average precipitation between April and June (Western Regional Climate Center). Thus, dispersal in slope habitat may occasionally be advantageous.

On a smaller temporal scale, effects of *P. virginiana* location, seed density and seed size were generally consistent for seed and seedling stages and may in part explain the clear differences in reproductive strategies between habitats. These results contrast with those of previous studies, which have documented substantial conflicts between the successive stages of establishment (Schupp 1995 and references therein; Houle 1998). Similar distance-dependent effects occurred for seeds and seedlings in each habitat. Although seed survival was density-dependent, seedling survival and growth were not influenced by any of the densities that were tested. Similarly, seed survival was greater away from versus along riparian corridors, but seedling stages were not affected by orientation (except for seedling emergence in a wet year). Seed size had variable effects on seed and seedling stages, but conflicts were minor when considered within the context of the appropriate environment. In riparian habitat, seed size had a weak positive effect on seedling growth, but had a strong negative effect on seed survival and a weak negative effect on seed germination. Because predation may be the primary mortality factor in this environment (Fig. 6a), the negative effect of seed size on survival is likely to outweigh any advantage of large seeds for seedling growth. In slope habitat, seed size also had a negative effect on seed survival, but had positive effects on seedling emergence, survival (in the soil moisture experiment) and growth. However, seed predation is relatively unimportant in this environment and desiccation is likely to be more limiting to seedlings than predation (Fig. 6b). Thus, positive effects of seed size on seedling establishment in slope habitat should outweigh negative effects on seed survival.

**Consequences of Dispersal Patterns for Offspring Recruitment**

*P. virginiana* seed rain was largely congruent with the most suitable locations for both seed and seedling establishment, in contrast with previous studies (e.g., Houle 1992; Herrera et al. 1994; Jordano and Herrera 1995; Schupp and Fuentes 1995 and references therein). As a result, initial patterns of seed dispersal should be a critical determinant of *P. virginiana* recruitment (Fig. 14b). In slope habitat, where most offspring are deposited and recruit under conspecifics, naturally-occurring adult *P. virginiana* occur in scattered dense clumps (Parson, pers. obs.). In riparian habitat, where most offspring disperse along corridors and recruit away from conspecifics, adult *P. virginiana* are less densely clumped and occur in a linear distribution along corridors (Parson, pers. obs.). However, seed dispersal in both habitats was not completely congruent with patterns of offspring establishment. In riparian habitat, seeds were rarely dispersed away from corridors, but this location was consistently associated with an increased chance of seed survival (Fig. 1c) and an increased chance of seedling emergence in one year (see above). In slope habitat, seeds were deposited under adult conspecifics, but the advantage of this location was strongest in average dry years (see above). The concordance between seed shadows and offspring establishment thus may fluctuate depending on variation in external factors such as levels of precipitation and predation intensity.

**SUMMARY: ARE SEED SIZE/NUMBER STRATEGIES ADAPTIVE?**

This investigation has provided new insight into the ecological and evolutionary influences on reproductive strategies for a single species of animal dispersed plant. Within local habitats, the patterns in which *P. virginiana* seeds are produced and deposited appear to be the patterns most conducive to offspring recruitment. To determine whether *P. virginiana* reproductive traits are currently adaptive, however, they must result in the highest fitness in a given environment when

compared with likely alternative phenotypes (Reeve and Sherman 1993). In addition, conditions that influence offspring establishment must similarly influence fitness of the maternal plant, and thus impose selection pressures on maternal plant reproductive strategies (Castro 1999; Donohue 1999). For riparian *P. virginiana*, the most plausible alternative reproductive strategy (given a resource tradeoff between seed size and number) is the production of relatively few, large seeds. Riparian plants with these traits are likely to have fewer seeds consumed by frugivores and dispersed away from adult conspecifics (Ch. 2). As a result, offspring of these plants will experience reduced survival and growth. Thus, the current reproductive strategy of *P. virginiana* in riparian habitat is likely to lead to greater offspring recruitment than the alternative strategy, despite the presence of tradeoffs during recruitment. Similarly, the most plausible alternative reproductive strategy of slope *P. virginiana* (i.e., production of many small seeds) is likely to result in greater seed consumption and dispersal away from adults (Ch. 2) and reduced seedling vigor. As a result, offspring produced by these plants will experience reduced emergence, survival, growth and overall recruitment relative to the current strategy. Differences in *P. virginiana* seed size and number between habitats are likely to maximize offspring fitness and thus may be an example of adaptive phenotypic plasticity of maternal plants (Via 1987; the failure to find ecotypic differentiation between similarly-sized seedlings from the two habitats indicates that seedlings may not be genetically distinct; Parson, unpubl. data).

The patterns documented for *P. virginiana* suggest that reproductive tradeoffs shift depending on the magnitude of biotic and abiotic stresses (Fig. 15). In environments with high levels of biotic stress (i.e., negative plant-plant or plant-animal interactions), the role that reproductive strategies plays in dispersal of offspring may be critical in order to move offspring away from negative effects of parent plants. Such conditions appear to occur for *P. virginiana* in riparian habitat. As levels of abiotic stress increase, however, the role of reproductive strategies in offspring establishment may become increasingly important to ensure that offspring can establish wherever

they happen to land. Dispersal of offspring may become less important or even undesirable in these conditions, since parent plants are likely to have positive effects overall on offspring establishment. Such conditions appear to occur for *P. virginiana* in slope habitat. This study thus is the first to demonstrate a shift in adult conspecific effects from negative to positive between environments. In addition, this study indicates that the dilemma between producing many small (i.e., dispersible) seeds versus few large (i.e., vigorous) seeds may occur among individuals or populations as well as among species. Continued examination of the effects of both seed-related traits and seed shadows on recruitment is critical to thoroughly understand how plants resolve the tradeoff between seed dispersibility and offspring survival and vigor. Ultimately, plant reproductive strategies influence not just maternal and offspring fitness and the evolution of plant life history tactics, but distributions of populations and species (e.g., Janzen 1970; Connell 1971; Platt and Weis 1985; Schupp et al. 1989; Barot et al. 1999).

## LITERATURE CITED

- Antonovics, J. and D. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Ann. Rev. Ecol. Syst.* 11: 411-452.
- Augspurger, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.* 71:759-771.
- Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *J. Ecol.* 72: 777-795.
- Augspurger, C. K., and K. Kitajima. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecol.* 73: 1270-1284.
- Barot, S., J. Gignoux and J. C. Menaut. 1999. Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. *Oikos* 86: 320-330.
- Berkowitz, A. R., C. D. Canham and V. R. Kelly. 1995. Competition versus facilitation of tree seedling growth and survival in early successional communities. *Ecol.* 76: 1156-1168.
- Bertness, M. D. and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecol. and Evol.* 9: 191-193.
- Bertness, M. D. and S. M. Yeh. 1994. Cooperative and competitive interactions in the recruitment of marsh elders. *Ecol.* 75: 2416-2429.
- Brown, J. H. and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecol.* 78: 1958-1965.
- Capinera, J. L. 1979. Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* 114: 350-361.

- Castro, J. 1999. Seed mass versus seedling performance in Scots pine: a maternally dependent trait. *New Phytol.* 144: 153-161.
- Chapman, C. A. and L. J. Chapman 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *J. Trop. Ecol.* 12: 491-504.
- Clark, D. A. and D. B. Clark. 1984. Spacing dynamics of a tropical rainforest tree: evaluation of the Janzen-Connell model. *Am. Nat.* 124: 769-788.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In: Den Boer, P. J. and G. Gradwell (eds). Dynamics of populations. PUDOC, Wageningen, pp. 298-312.*
- Connell, J. H. and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- Connell, J. H. 1979. Tropical rainforests and coral reef as open non-equilibrium systems. *In: Anderson, M. R., B. C. Turner and L. R. Taylor (eds.). Population dynamics. Blackwell, Oxford.*
- Debussche, M. and P. Isenmann. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69: 414-426.
- DeSimone, S. A. and P. H. Zedler. 1999. Shrub seedling recruitment in unburned californian coastal sage scrub and adjacent grassland. *Ecol.* 80: 2018-2032.
- Diaz, I., C. Papic and J. J. Armesto. 1999. An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiloe Island, Chile. *Oikos* 87: 228-238.
- Dirzo, R. and C. A. Dominguez. 1986. Seed shadows, seed predation and the advantages of dispersal. *In: Estrada, A. and T. H. Fleming (eds.). Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht.*
- Dolan, R. W. 1984. The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa* (Onagraceae). *Am. J. Bot.* 71: 1302-1307.



- Donohue, K. 1999. Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *Am. Nat.* 154: 674-689.
- Ellner, S. and A. Shmida. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* 51: 133-144.
- Forget, P. M. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpiniaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26: 408-419.
- Foster, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Bot. Rev.* 52: 260-299.
- Fuentes, E. R., R. D. Otaiza, M. C. Alliende, A. Hoffman and A. Poiani. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* 62: 405-411.
- Fuentes, E. R., A. J. Hoffman, A. Poiani, and M. C. Alliende. 1986. Vegetation change in large clearings: patterns in the Chilean matorral. *Oecologia* 68: 358-366.
- Germaine, H. L. and G. R. McPherson. 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower tree line. *Ecoscience* 74: 68-82.
- Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monogr.* 61: 183-206.
- Gross, K. L. and A. D. Smith. 1991. Seed mass and emergence time effects on performance of *Panicum dichotomiflorum* Michx. across environments. *Oecologia* 87: 270-278.
- Herrera, C. M., P. Jordano, L. Lopez-Soria and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.* 64: 315-344.
- Holmgren, M., M. Scheffer and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecol.* 78: 1966-1975.

- Horvitz, C. C. and D. W. Schemske. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecol.* 75: 1949-1958.
- Horvitz, C. C. and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol. Monogr.* 65: 155-192.
- Houle, G. H. 1992. Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *J. Ecol.* 80: 99-108.
- Houle, G. H. 1998. Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. *Ecol.* 79: 807-818.
- Howe, H. F. 1990. Survival and growth of juvenile *Virola surinamensis* in Panama: Effects of herbivory and canopy closure. *J. Tropical Ecol.* 6: 259-280.
- Howe, H. F. 1993. Aspects of variation in a neotropical seed dispersal system. *Vegetatio* 107/108: 149-162.
- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecol.* 66: 781-791.
- Hubbard, J. A. and G. R. McPherson. 1999. Do seed predation and dispersal limit downslope movement of a semi-desert grassland/oak woodland transition? *J. Veg. Sci.* 10: 739-744.
- Hulme, P. E. 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia* 111: 91-98.
- Hulme, P. E. 1998. Post-dispersal seed predation and seed bank persistence. *Seed Sci. Res.* 8: 513-519.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 521-528.

- Jordano, P. and C. M. Herrera. 1995. Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2: 230-237.
- Kaspari, M. 1993. Removal of seeds from neotropical frugivore droppings: ant responses to seed number. *Oecologia* 95: 81-88.
- Keddy, P. A. 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia* 32: 348-355.
- Kollmann, J. and P. J. Grubb. 1999. Recruitment of fleshy-fruited species under different shrub species: Control by under-canopy environment. *Ecol. Res.* 14: 9-21.
- Manga, V. K. and O. P. Yadav. 1995. Effect of seed size on developmental traits and ability to tolerate drought in pearl millet. *J. Arid. Environ.* 29: 169-172.
- McAuliffe, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects on saguaros. *Oecologia* 64: 319-321.
- McGinley, M. A. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.* 130: 370-398.
- Mittelbach, G. G. and K. L. Gross. 1984. Experimental studies of seed predation in old-fields. *Oecologia* 65: 7-13.
- Morse, D. H. and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. *Oecologia* 67: 372-379.
- Myster, R. W. and S. T. A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree and seed predation in old fields. *Oikos* 66: 381-388.
- Platt, W. J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). *Oecologia* 22: 399-409.
- Podolsky, R. H. and M. V. Price. 1990. Patch use by *Dipodomys deserti* (Rodentia: Heteromyidae): profitability, preference, and depletion dynamics. *Oecologia* 83: 83-90.

- Reeve, H. K. and P. W. Sherman. 1993. Adaptation and the goals of evolutionary research. *Quart. Rev. Biol.* 68: 1-32.
- Roff, D. A. 1992. The evolution of life histories. Routledge, Chapman and Hall, New York.
- Russell, S. K. and E. W. Schupp. 1998. Effect of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). *Oikos* 81: 434-443.
- Schupp, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76: 525-530.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82: 399-409.
- Schupp, E. W. and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2: 267-275.
- Schupp, E. W., H. F. Howe, C. K. Augspurger and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70: 562-564.
- Shaw, R.G. and J. Antonovics. 1986. Density-dependence in *Salvia lyrata*, a herbaceous perennial: the effects of experimental alteration of seed densities. *J. Ecol.* 74: 797-813.
- Silva Matos, D. M., R. P. Freckleton and A. R. Watkinson. 1999. The role of density dependence in the population dynamics of a tropical palm. *Ecol.* 80: 2635-2650.
- Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecol.* 68:1341-1350.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46: 337-365.
- Stanton, M. L. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia* 67: 524-531.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quart Rev Biol* 51: 3-49.

- Suding, K. N. and D. E. Goldberg. 1999. Variation in the effects of vegetation and litter on recruitment across productivity gradients. *J. Ecol.* 87: 436-449.
- Turnbull, L. A., M. Rees and M. J. Crawley. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899-912.
- Venable, D. L. and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131: 360-384.
- Via, S. 1987. Genetic constraints on the evolution of phenotypic plasticity. Pp. 46-71 *In*: V. Loeschcke (ed.), Genetic constraints on adaptive evolution. Springer, Berlin.
- Webb, L. J., J. G. Tracey, and K. P. Haydock. 1967. A factor toxic to seedlings of the same species associated with living roots of the non-gregarious subtropical rainforest tree *Grevillea robusta*. *J. Appl. Ecol.* 4: 13-25.
- Webb, S. L., and M. F. Willson. 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67: 150-153.
- Weid, A. and C. Galen. 1998. Plant parental care: conspecific nurse effects in *Frasera speciosa* and *Cersium scopulorum*. *Ecol.* 79: 1657-1668.
- Weltzin, J. F. and G. R. McPherson. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecol. Monogr.* 69: 513-534.
- Whelan, C. J., M. F. Willson, C. A. Tuma and I. Souza-Pinto. 1991. Spatial and temporal patterns of post-dispersal seed predation. *Can. J. Bot.* 69: 428-36.
- Willson, M. F. 1992. The ecology of seed dispersal. *In*: M. Fenner (ed.), The ecology of regeneration in plant communities. C.A.B. International, Southampton, UK.
- Willson, M. F., and C. J. Whelan. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: Effects of density, habitat, location, season, and species. *Oikos* 57: 191-198.

Wilson, S. D. 1998. Competition between grasses and woody plants. *In*: Cheplick, G. P. (ed.).

Population biology of grasses. Cambridge Univ. Press, Cambridge, UK.

Winn, A. A. 1988. Ecological and evolutionary consequences of seed size in *Prunella vulgaris*.

*Ecology* 69: 1537-1544.

Wulff, R. D. 1986. Seed size variation in *Desmodium paniculatum*: II. Effects on seedling growth and physiological performance. *J. Ecol.* 74: 99-114.

**Table 1.** Kruskal-Wallis independent samples results for the effect of distance from *P. virginiana* canopy, seed density, and orientation with respect to riparian corridor on seed removal rates, 1996-1998.

Habitat							
Variable	Year	Riparian			Slope		
		N	X <sup>2</sup>	P <sup>a</sup>	N	X <sup>2</sup>	P <sup>a</sup>
Year	---	272	19.15	0.0013	245	7.46	0.43
Distance	1996	86	3.79	1.00	66	0.012	1.00
	1997	81	7.24	0.49	81	3.69	1.00
	1998	75	14.37	0.014	77	2.00	1.00
Density	1996	86	1.21	1.00	66	1.19	1.00
	1997	81	2.26	1.00	81	0.66	1.00
	1998	75	1.07	1.00	77	2.04	1.00
Orientation	1996	54	0.84	1.00	---	---	---
	1997	46	0.48	1.00	---	---	---
	1998	36	0.14	1.00	---	---	---

<sup>a</sup> Significant tests of year, distance, density and orientation indicated in bold (tested along with three tests of habitat; p-values have been multiplied by 20).

**Table 2.** Kruskal-Wallis independent samples results for effects of distance from *P. virginiana* canopy, seedling density, and orientation with respect to riparian corridor on the proportion of seedlings that survived per plot, 1997-1999.

Variable	Year	Riparian			Habitat		
		N	X <sup>2</sup>	P <sup>a</sup>	N	X <sup>2</sup>	P <sup>a</sup>
Year	---	<b>245</b>	<b>17.37</b>	<b>0.0031</b>	<b>203</b>	<b>55.57</b>	<b>&lt;0.0005</b>
Distance	1997	43	1.49	1.00	51	0.25	1.00
	1998	<b>75</b>	<b>16.83</b>	<b>0.0040</b>	68	1.16	1.00
	1999	127	9.21	0.18	<b>84</b>	<b>19.66</b>	<b>&lt;0.0005</b>
Density	1998	63	2.96	1.00	61	1.20	1.00
	1999	95	0.38	1.00	58	0.51	1.00
Orientation	1997	28	0.11	1.00	---	---	---
	1998	50	0.44	1.00	---	---	---
	1999	97	0.13	1.00	---	---	---

<sup>a</sup> Significant tests of year, distance and density indicated in bold (tested along with three tests of habitat; p-values have been multiplied by 18).



**Table 3.** Multivariate ANOVA results (using Pillai's trace) for effects of habitat, distance, seed size and all significant two-way interactions on seedling growth (i.e., mm height growth/day, mm<sup>2</sup> leaf growth/day and number of leaves, mg of total mass/day and root mass:shoot mass ratios) in 1998 and 1999. Mass and root:shoot ratios were not measured in 1998. Early growth rates (i.e., Height 1, Leaf Area 1) were calculated between emergence and 1 week of age, and late growth rates (i.e., Height 2, Leaf Area 2) between 1 and 4 weeks of age. Number of leaves was censused at 4 weeks of age, and mass and root:shoot ratios were censused at 10 weeks of age.

Year	Factors	F	df <sup>a</sup>	P <sup>b</sup>	Dependent variables significant in univariate tests <sup>c</sup>
1998	<b>Habitat</b>	<b>6.19</b>	5, 80	<b>&lt;0.0005</b>	Height 1, Height 2
	<b>Distance</b>	<b>12.55</b>	5, 80	<b>&lt;0.0005</b>	Height 1, Leaf Area 2, # Leaves
	<b>Size</b>	<b>4.56</b>	10, 162	<b>&lt;0.0005</b>	Leaf Area 1, Leaf Area 2
	<b>Hab*Dist</b>	<b>6.61</b>	5, 80	<b>&lt;0.0005</b>	Height 1
1999	<b>Habitat</b>	<b>5.84</b>	7, 51	<b>&lt;0.0005</b>	Height 2
	<b>Distance</b>	<b>6.49</b>	7, 78	<b>&lt;0.0005</b>	Height 2, Leaf Area 2
	<b>Size</b>	1.90	14, 104	0.07	(None)
	<b>Hab*Dist</b>	<b>4.79</b>	7, 78	<b>0.0007</b>	Height 1

<sup>a</sup> Group and error df, respectively

<sup>b</sup> Significant tests indicated in bold type (p-values have been multiplied by 2).

<sup>c</sup> P-values were multiplied by 5 for 1998 data and by 7 for 1999 data. In 1999, error variances were not equal across groups for Height 1 and root:shoot ratios.

**Table 4.** Multivariate ANOVA results (using Pillai's trace) for effects of habitat, water treatment, distance, seed size and all significant two-way interactions on seedling growth (i.e., mm height growth/day, mm<sup>2</sup> leaf growth/day, number of leaves, mg of total mass/day and root mass:shoot mass ratios), 1999. Early growth rates (i.e., Height 1, Leaf Area 1) were calculated between emergence and 1 week of age, and late growth rates (i.e., Height 2, Leaf Area 2) between 1 and 4 weeks of age. Number of leaves was censused at 4 weeks of age, and mass and root:shoot ratios were censused at 10 weeks of age.

Factors	F	df <sup>a</sup>	P <sup>b</sup>	Dependent variables significant in univariate tests <sup>c</sup>
<b>Habitat</b>	<b>7.85</b>	7, 75	<b>&lt;0.0005</b>	Height 2, Leaf Area 2, Root:Shoot (None)
Water	1.18	7, 75	0.32	
<b>Distance</b>	<b>10.48</b>	7, 75	<b>&lt;0.0005</b>	Leaf Area 2, # Leaves, Mass
<b>Size</b>	<b>3.11</b>	14, 152	<b>&lt;0.0005</b>	# Leaves, Mass
<b>Hab*Water</b>	<b>2.59</b>	7, 75	<b>0.019</b>	(None)
<b>Water*Dist</b>	<b>3.33</b>	7, 75	<b>0.004</b>	Height 2, Mass

<sup>a</sup> Group and error df, respectively

<sup>b</sup> Significant tests indicated in bold.

<sup>c</sup> P-values were multiplied by 7. Error variances were not equal across groups for root:shoot ratios.

**Table 5.** Multivariate ANOVA results (using Pillai's trace) for effects of habitat, protection treatment, distance relative to *P. virginiana* canopies and all significant two-way interactions on seedling growth (i.e., mm height growth/day, mm<sup>2</sup> leaf growth/day and number of leaves), 1999. Early growth rates (i.e., Height 1, Leaf Area 1) were calculated between emergence and 4 weeks after planting, and late growth rates (i.e., Height 2, Leaf Area 2) between 4 and 7 weeks after planting; number of leaves was censused at week 7.

Factors	F	df <sup>a</sup>	P <sup>b</sup>	Dependent variables significant in univariate tests <sup>c</sup>
<b>Habitat</b>	<b>3.37</b>	7, 27	<b>0.01</b>	Height 2
Protection	1.61	7, 27	0.17	(None)
<b>Distance</b>	<b>7.19</b>	7, 27	<b>&lt;0.0005</b>	Leaf Area 2, Root:Shoot
<b>Hab*Dist</b>	<b>3.99</b>	7, 27	<b>0.004</b>	Root:Shoot

<sup>a</sup> Group and error variances, respectively

<sup>b</sup> Significant tests indicated in bold

<sup>c</sup> P-values were multiplied by 7. Error variances were not equal across groups for Height 1.

## FIGURE LEGENDS

**Figure 1.** Proportion of plots detected by seed predators in riparian and slope habitat **(a)** during three consecutive years, and **(b)** at three distances from *P. virginiana* canopies, 1996-1998. In a Logistic Regression (p-values multiplied by 4): Deviance (i.e., change in  $-2 \log$  likelihood if each covariate is removed individually from the model) = 33.87,  $P < 0.0005$  (Year effect); Deviance = 0.52,  $P = 1.00$  (Habitat effect); Deviance = 0.25,  $P = 1.00$  (Distance effect); Deviance = 17.30,  $P = 0.0002$  (Habitat\*Distance effect). Significant within-habitat differences in posthoc tests are indicated by different lower-case letters. **(c)** Proportion of plots detected by seed predators in riparian habitat at two distances from *P. virginiana* canopies and two orientations with respect to riparian corridors, 1996-1998. In a Logistic Regression (p-values multiplied by 4): Deviance = 13.25;  $P = 0.0011$  (Orientation effect).

**Figure 2.** Seed removal rates (i.e., % of seeds removed daily from detected plots) in riparian and slope habitat **(a)** during three consecutive years, and **(b)** at three distances from adult *P. virginiana* canopies, 1996-1998. Significant within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 3.** Difference between the percent of large and small seeds removed by predators from plots in riparian and slope habitat, 1998. In a paired Samples *t*-test;  $t = 5.35$ ;  $df = 17$ ;  $P < 0.0005$ . Significant differences from zero are indicated by asterisks.

**Figure 4.** **(a)** Proportion of *P. virginiana* seedlings that emerged per plot at three distances from *P. virginiana* canopy in riparian and slope habitat, 1997 – 1999. In a G. F. ANOVA (p-values multiplied by 2):  $F_{2, 330} = 4.24$ ,  $P = 0.03$  (Distance effect);  $F_{2, 330} = 7.26$ ,  $P = 0.002$  (Habitat\*Distance effect). **(b)** Proportion of *P. virginiana* seedlings that emerged per plot along

and away from riparian corridors in riparian habitat (all plots located 5 - 15 m away from *P. virginiana* canopies), 1997 – 1999. In a G. F. ANOVA (p-values multiplied by 2):  $F_{2, 115} = 6.67$ ,  $P = 0.03$  (Orientation\*Year effect). In both ANOVA's, plots in which no seedlings emerged were excluded to obtain normal distributions, but error variances were not equal across groups. Significant within-year or within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 5.** Percent of *P. virginiana* seedlings that survived per plot in riparian and slope habitat (a) during three consecutive years (in Kruskal-Wallis tests (p-values multiplied by 18):  $X^2 = 0.38$ ,  $P = 1.00$  (1997);  $X^2 = 22.32$ ,  $P < 0.0005$  (1998);  $X^2 = 35.98$ ,  $P < 0.0005$  (1999)); (b) at three distances from *P. virginiana* canopies, 1998, and (c) at three distances from *P. virginiana* canopies, 1999. Significant within-year or within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 6.** Percent of *P. virginiana* seedlings that died per plot as a result of predation or desiccation (of all seedlings that died as a result of one of these factors), in (a) 1998 and (b) 1999. In Wilcoxon Signed Ranks Tests (p-values multiplied by 4);  $Z = 5.83$ ;  $N = 48$ ;  $P < 0.0005$  (1998 Riparian);  $Z = 0.033$ ;  $N = 39$ ;  $P = 1.00$  (1998 Slope);  $Z = 2.17$ ;  $N = 37$ ;  $P = 0.12$  (1999 Riparian);  $Z = 6.25$ ;  $N = 48$ ;  $P < 0.0005$  (1999 Slope). Significant within-habitat differences are indicated by different lower-case letters.

**Figure 7.** Proportion of *P. virginiana* seedlings from three sizes of seeds that emerged from protected plots in riparian and slope habitats, 1997 – 1999. In a G. F. ANOVA (p-values multiplied by 2):  $F_{2, 414} = 4.97$ ,  $P = 0.015$  (Size effect). Significant within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 8. (a)** Average rate of height growth (mm/day) between emergence and 1 week of age for plots of seedlings from three sizes of seeds in riparian and slope habitat, 1999. **(b)** Average number of leaves per 4-week-old seedling for plots of seedlings from three sizes of seeds in riparian and slope habitat, 1999. Significant within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 9.** Average rate of total seedling growth (above + belowground mg/day) for plots of seedlings from three sizes of seeds. Seedlings were measured between emergence and **(a)** 10 weeks (seedlings planted in 1999; see Table 3 for MANOVA results), or **(b)** 13 months (seedlings planted in 1997 and 1998; both years combined because growth did not differ). In a G. F. ANOVA (p-values multiplied by 6):  $F_{2, 135} = 10.05$ ;  $P < 0.0005$  (Size effect);  $F_{1, 135} = 3.62$ ;  $P = 0.35$  (Year effect);  $F_{1, 135} = 2.49$ ;  $P = 0.72$  (Habitat effect);  $F_{1, 135} = 31.69$ ;  $P < 0.0005$  (Distance effect); Significant within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 10. (a)** Proportion of *P. virginiana* seedlings in two water treatments that emerged in protected plots in riparian and slope habitats, 1999. In a G.F. ANOVA:  $F_{1, 143} = 3.08$ ;  $P = 0.081$  (Habitat effect);  $F_{1, 143} = 4.57$ ;  $P = 0.034$  (Water effect);  $F_{1, 143} = 3.08$ ;  $P = 0.081$  (Distance effect);  $F_{2, 143} = 7.47$ ;  $P = 0.001$  (Size effect);  $F_{1, 143} = 8.12$ ;  $P = 0.005$  (Habitat\*Water effect). **(b)** Proportion of *P. virginiana* seedlings in two water treatments that survived in protected plots in riparian and slope habitat, 1999. In Kruskal-Wallis tests (p-values multiplied by 8):  $X^2 = 0.21$ ;  $N = 88$ ;  $P = 1.00$  (Water effect, riparian habitat);  $X^2 = 9.39$ ;  $N = 59$ ;  $P = 0.018$  (Water effect, slope habitat). Significant within-habitat differences in posthoc tests are indicated by different lower-case letters.

**Figure 11.** Proportion of *P. virginiana* seedlings from three sizes of seeds and in two water treatments that survived in protected plots in (a) riparian and (b) slope habitat, 1999. In Kruskal-Wallis tests (p-values multiplied by 8):  $X^2 = 6.44$ ;  $N = 20$ ;  $P = 0.088$  (Water effect, slope habitat, small seeds);  $P > 0.50$  for tests of all other habitat/seed size combinations. Significant within-treatment differences are indicated by different lower-case letters.

**Figure 12.** Predawn xylem pressure potentials (PDXPP) of *P. virginiana* seedlings at two distances relative to adult *P. virginiana* canopies in riparian and slope habitat, July 1999. In Kruskal-Wallis tests (p-values multiplied by 3):  $X^2 = 14.46$ ;  $N = 20$ ;  $P < 0.0005$  (Habitat effect);  $P = 1.00$  for distance effects within habitats.

**Figure 13.** Probability of seedling establishment (i.e., percent seed survival/day \* germination \* emergence \* seedling survival) for small ( $\leq 5.3$  mm diameter) or large-sized seeds ( $\geq 6.35$  mm diameter) in riparian and slope habitat; 1997 – 1999. Proportions obtained in the seedling location experiment were multiplied by ratios obtained from the seed size experiment (i.e., small:medium-sized seed proportions and large:medium-sized seed proportions), and were averaged between distances and habitats if differences between sizes were not significant. Medium-sized seeds were not included because seed survival and germination estimates were not obtained for this size.

**Figure 14.** (a) Probability of deposition of processed seeds (i.e., seeds with fruit pulp removed by frugivores; hatched bars) and seedling establishment (i.e., percent seed survival/day \* germination \* emergence \* seedling survival; white and gray bars) at two distances relative to *P. virginiana* canopy in riparian and slope habitat. Data from all years were combined, and were averaged between habitats or distances if differences did not approach significance. (b) Estimated number of successfully recruited seedlings per year (i.e., average number of seeds per plant \*

percent processed by frugivores \* percent deposited \* percent seedling establishment; all numbers may be overestimates because information on total seed survival was not available) at two distances relative to *P. virginiana* canopy in riparian and slope habitat.

**Figure 15.** Hypothetical diagram of the relative importance of seed size and number for seed dispersal and seedling establishment of plants growing in contrasting environmental conditions (i.e., environments with relatively large biotic versus abiotic effects).



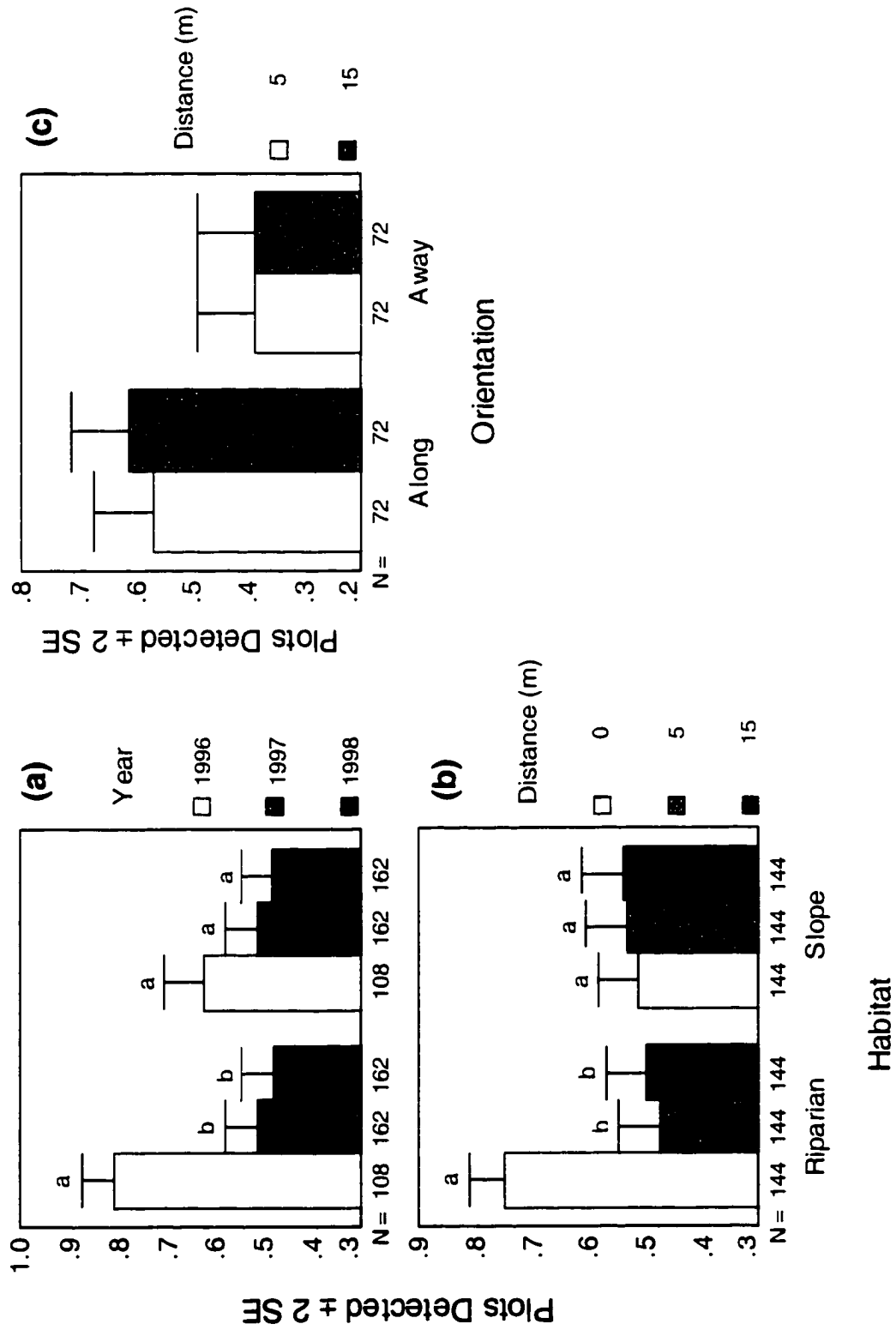


FIGURE 1

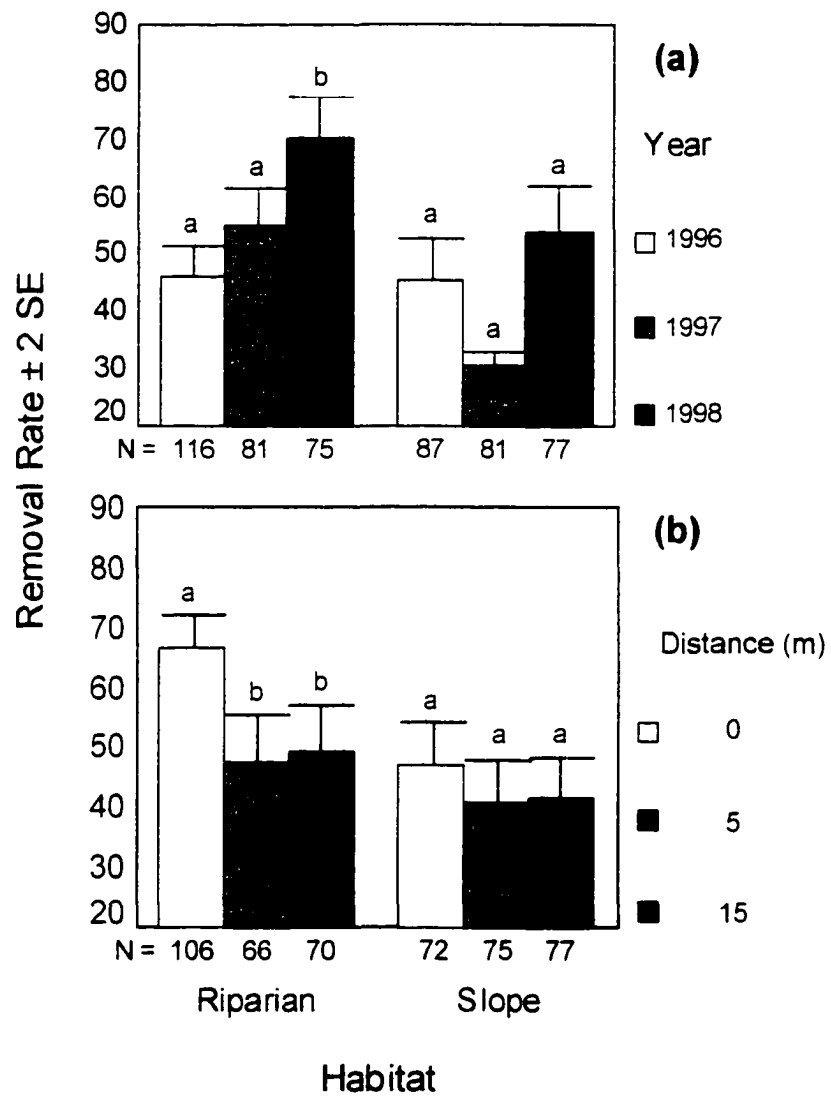
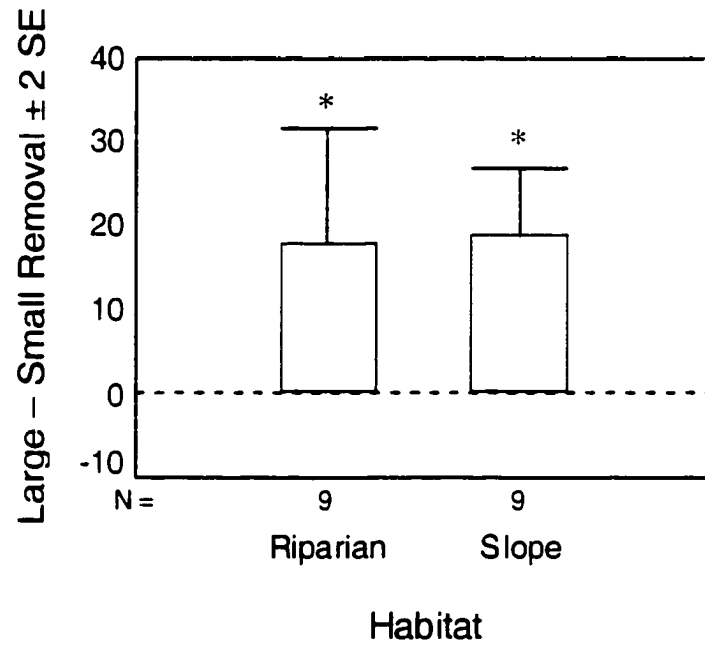


FIGURE 2



**FIGURE 3**

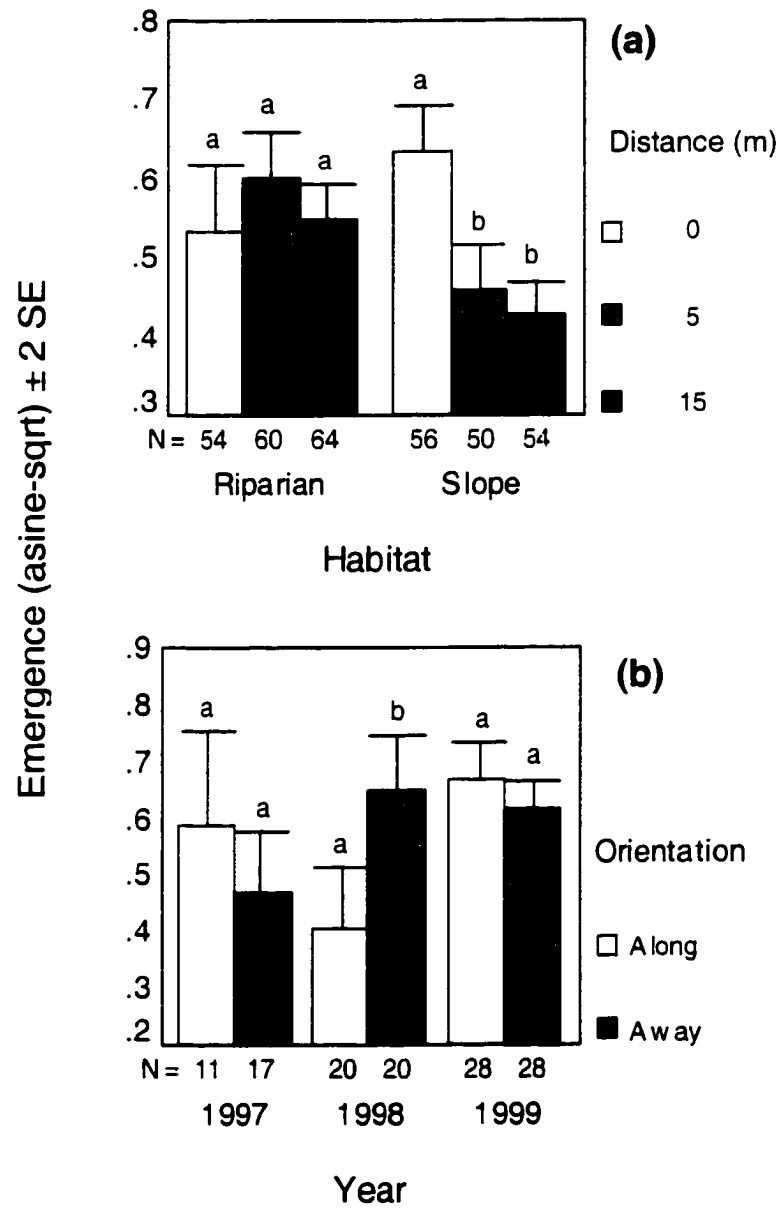


FIGURE 4

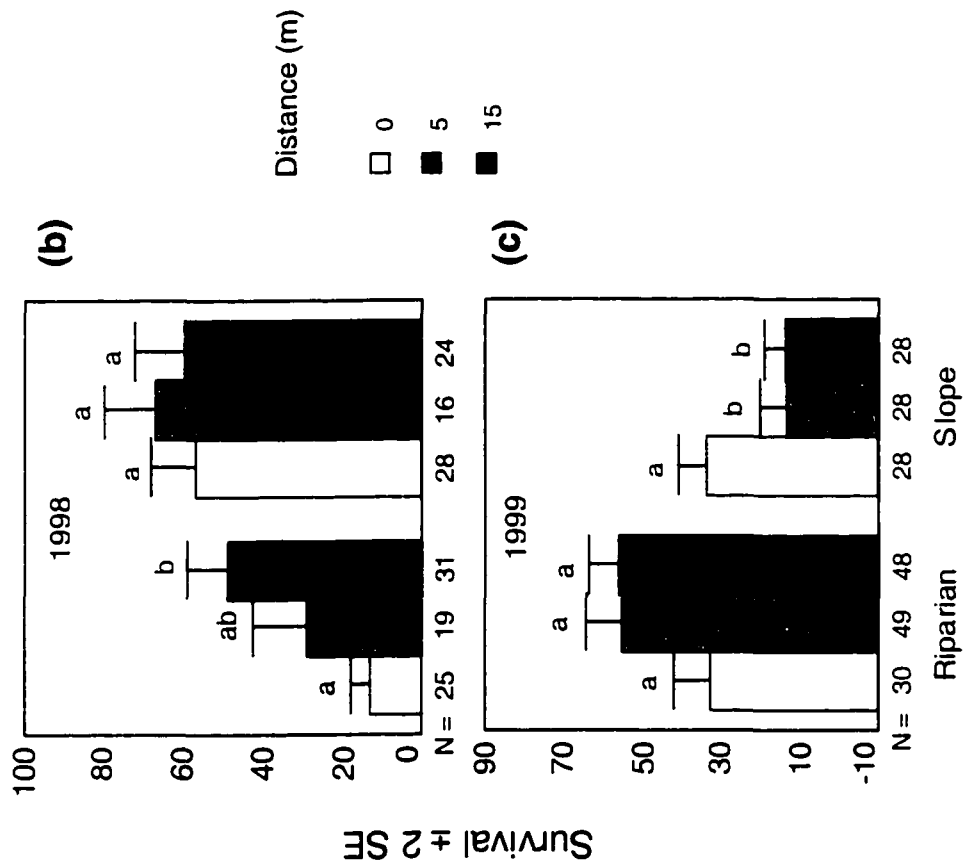
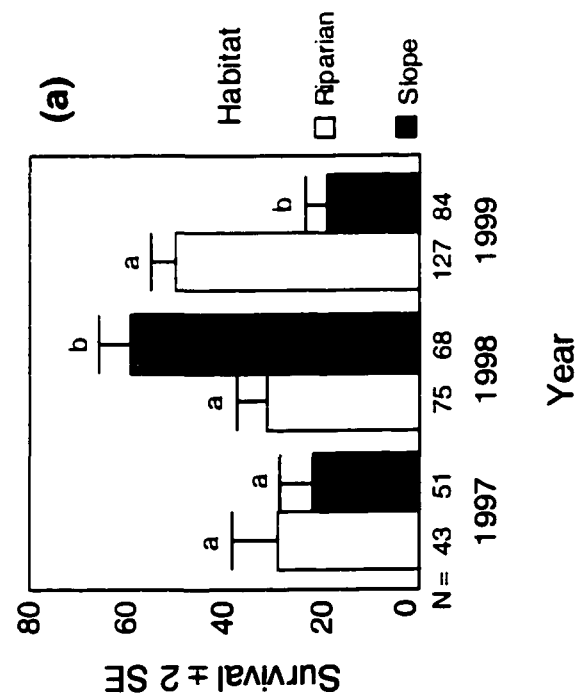


FIGURE 5

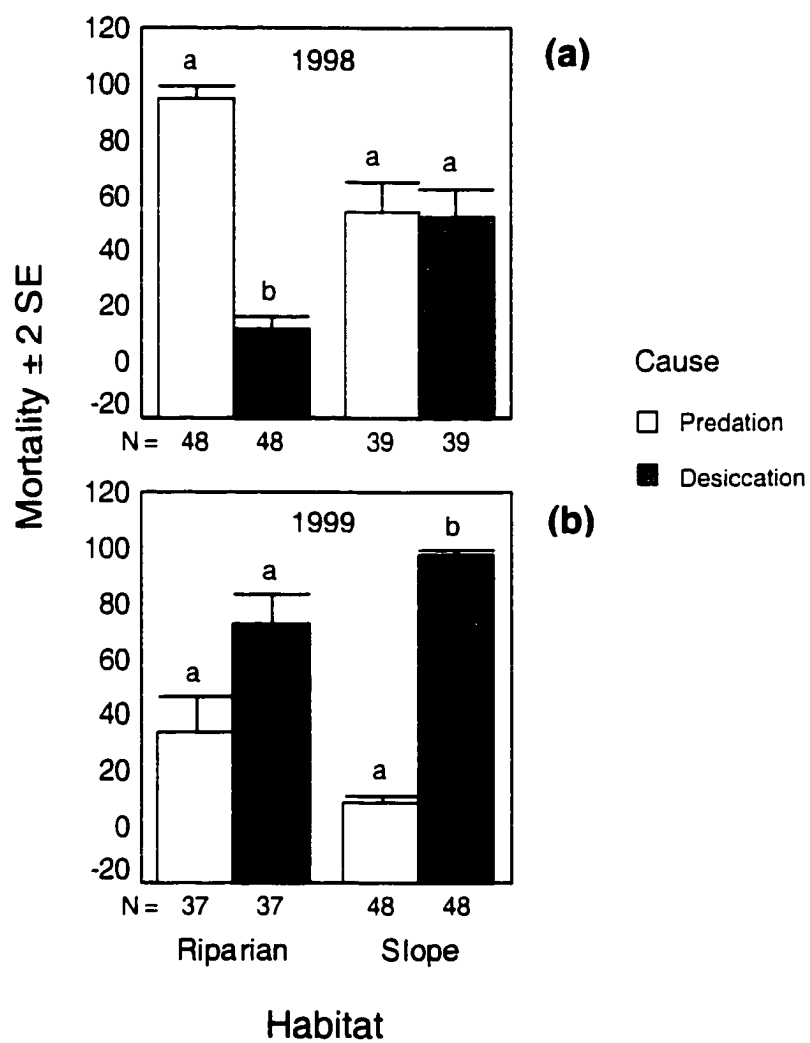
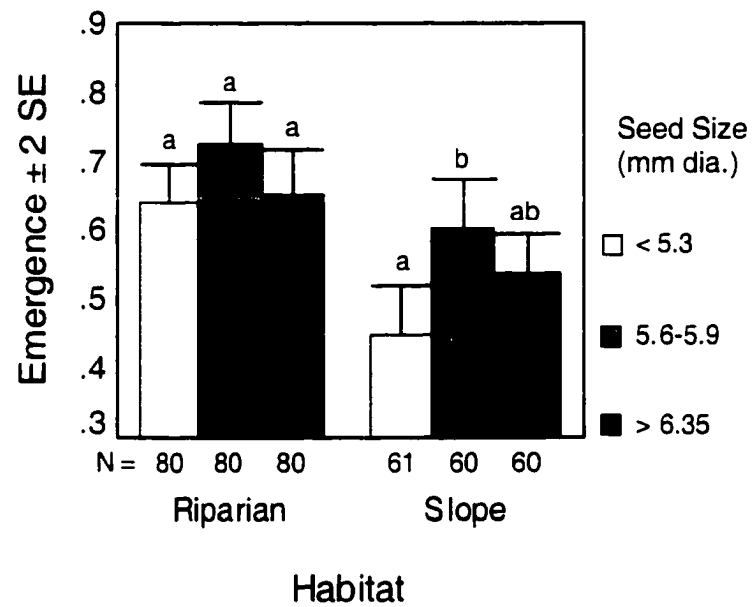


FIGURE 6

**FIGURE 7**

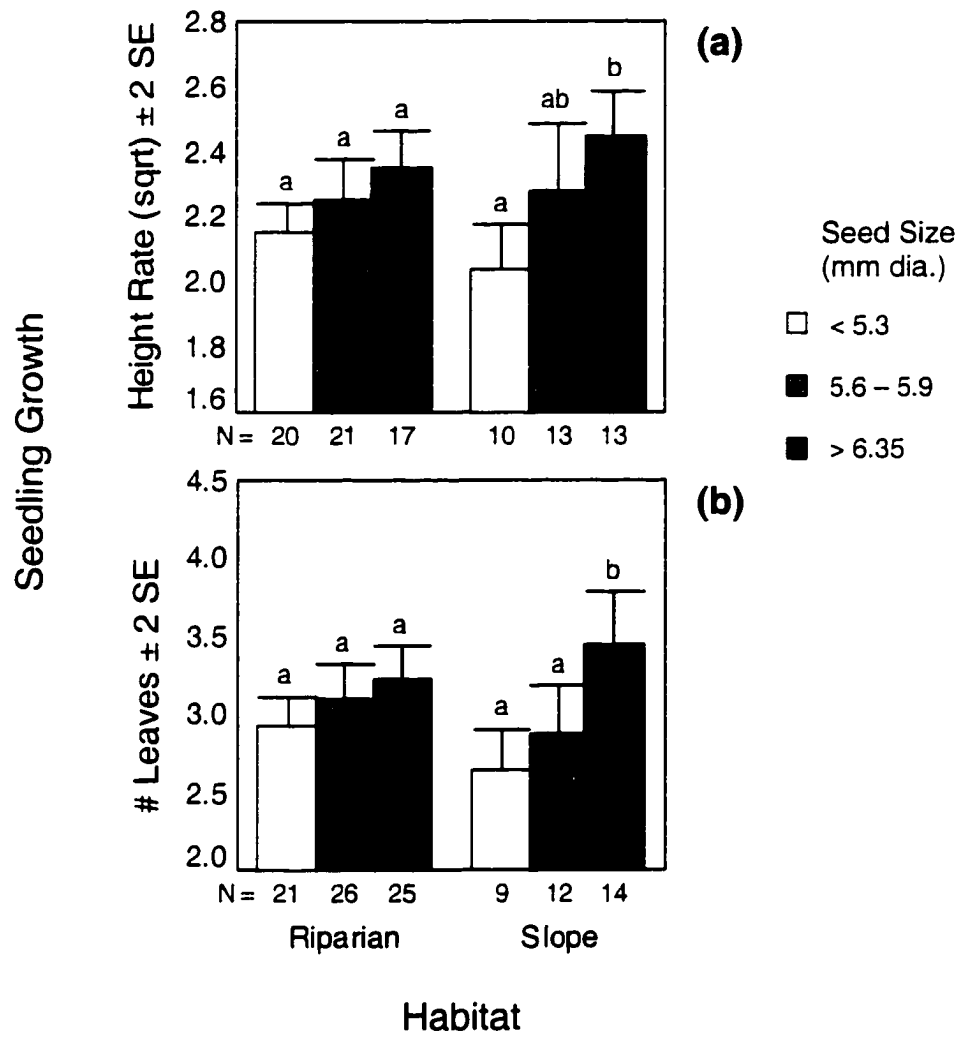


FIGURE 8



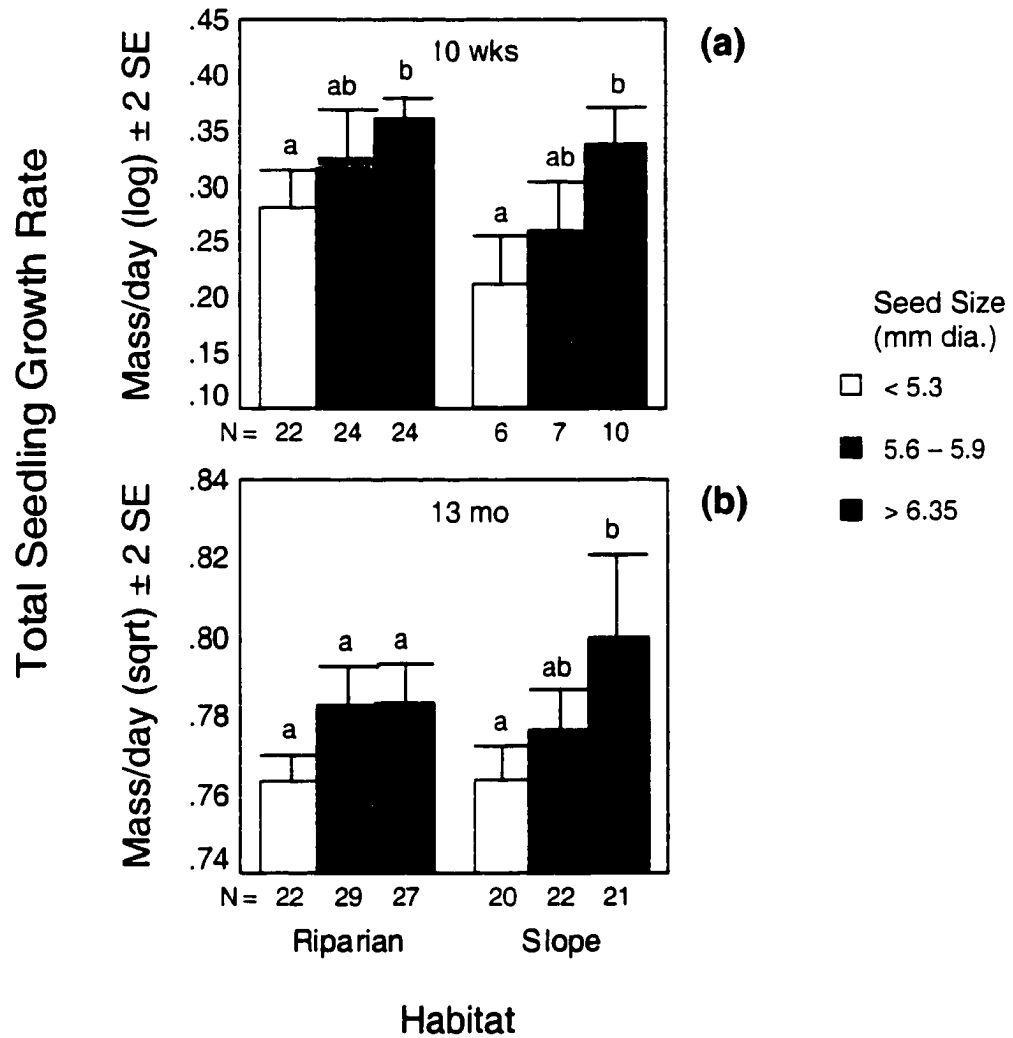


FIGURE 9

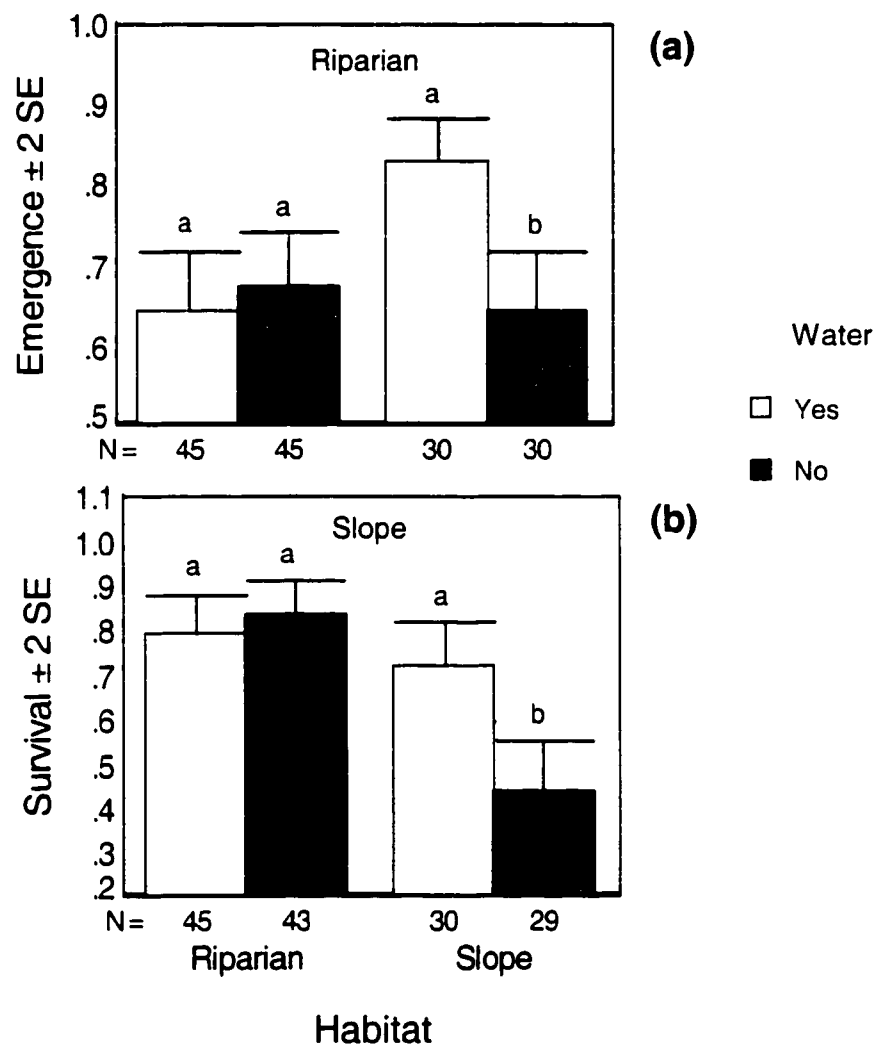


FIGURE 10

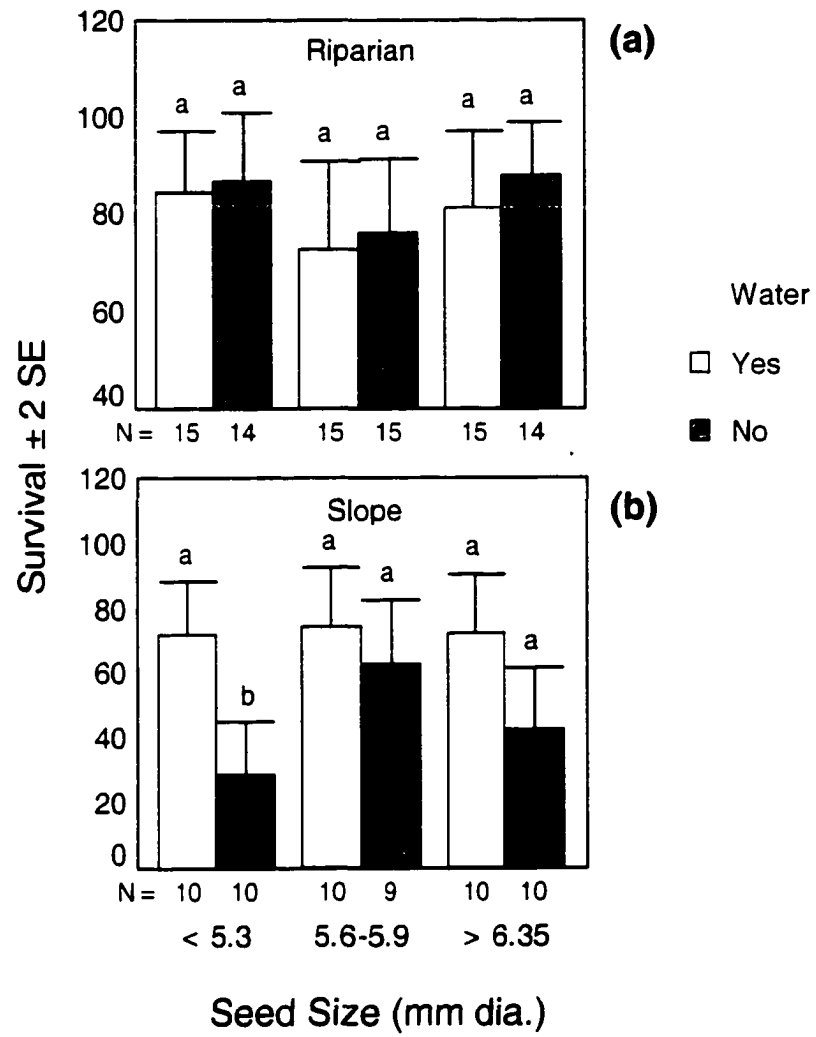


FIGURE 11

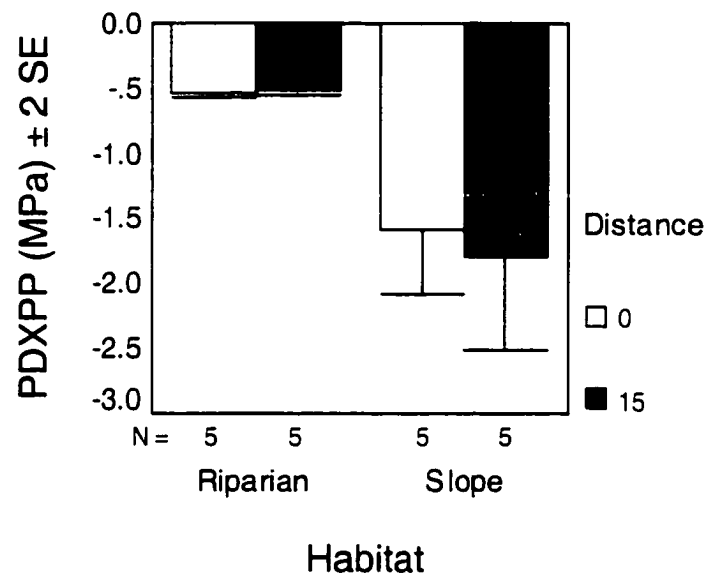
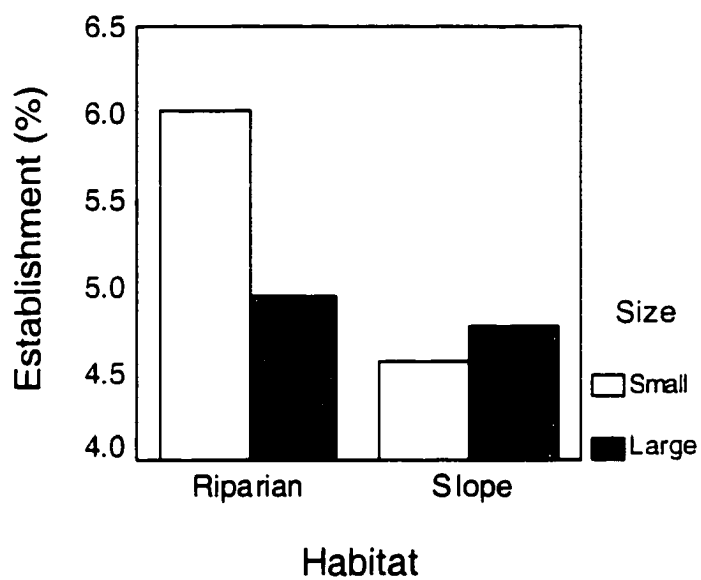


FIGURE 12

**FIGURE 13**

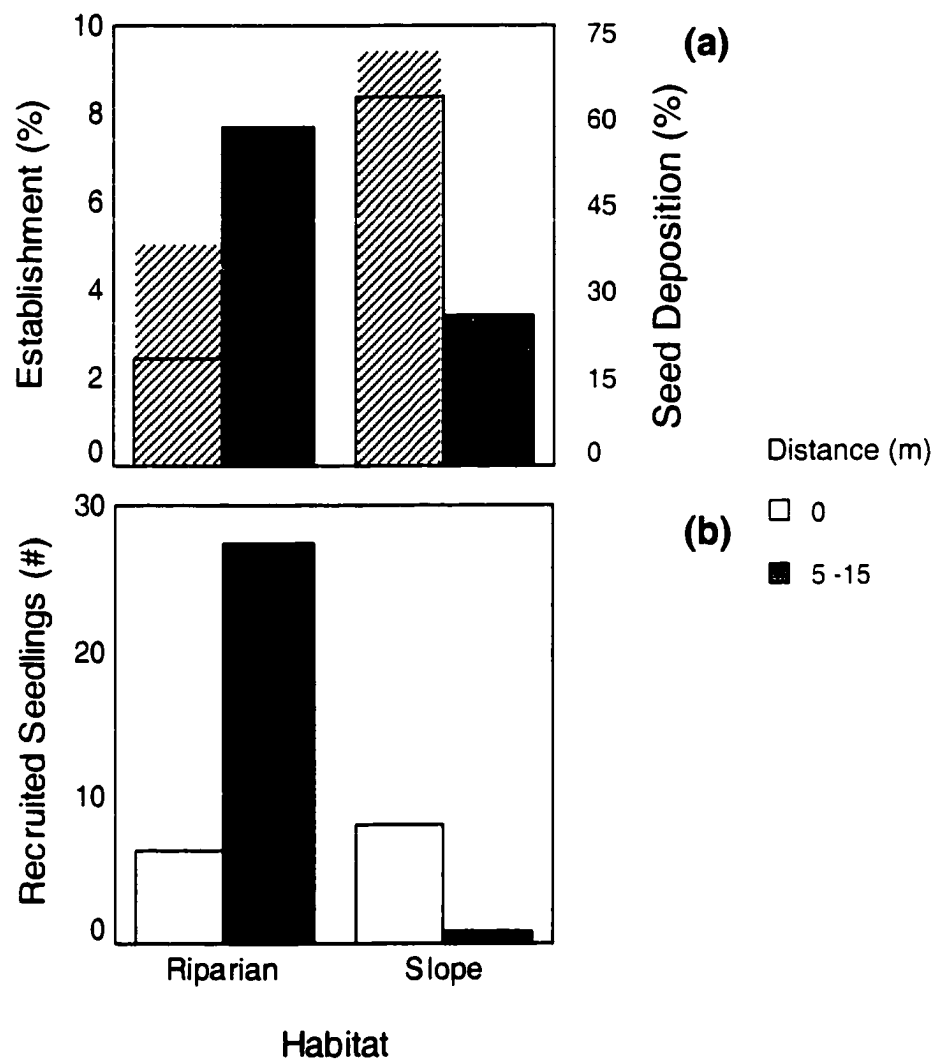


FIGURE 14

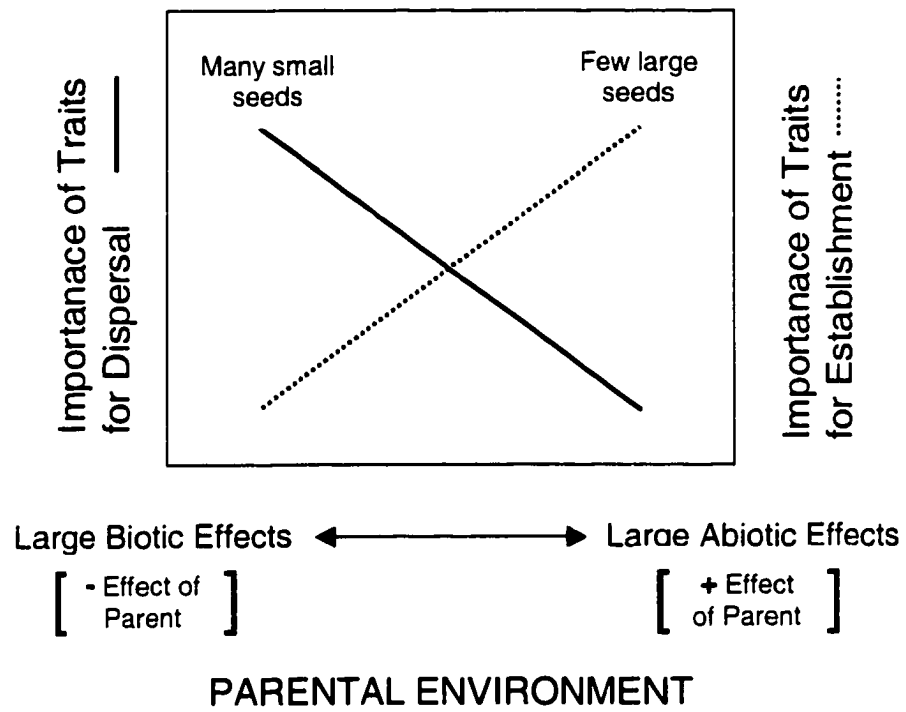


FIGURE 15